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UNDERSTANDING THE EFFICACY OF FISH LADDER USE BY ALEWIFE (ALOSA PSEUDOHARENGUS)

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UNDERSTANDING THE EFFICACY OF FISH LADDER USE BY ALEWIFE (*ALOSA PSEUDOHARENGUS*)

BY

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DEDICATION

This thesis is dedicated to my family who has always supported me in every endeavor. My wife Leigh, sons Fisher and Riley, brother Michael, father Rickey, and most importantly, in loving memory to my mother

Patricia Ann Sullivan

(May 1958–October 1996).

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ABSTRACT

UNDERSTANDING THE EFFICACY OF FISH LADDER USE BY ALEWIFE (*ALOSA PSEUDOHARENGUS*)

by

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University of New Hampshire, September, 2017

River herring, the collective name given to North American populations of Alewife (*Alosa pseudoharengus*) and Blueback Herring (*A. aestivalis*), are iteroparous, anadromous members of the family Clupeidae, with similar morphology, ecological roles, and overlapping distributions. Once abundant in coastal rivers of New Hampshire, many factors including commercial fishing, habitat degradation, and dam construction resulted in a precipitous decline of the species along the entire coast. Successful efforts to restore populations have included the construction of fish ladders at dams. However, fish ladders require constant operation and maintenance to efficiently pass river herring, and only provide access to spawning habitat up to the next barrier, all too often, man-made.

Alewife passage efficiency in fish ladders of all designs has received little attention historically, but is important to understand how to interpret annual counts, that for many rivers are the only index used in current stock assessments. In this study, passive integrated transponder (PIT) tags were used to assess the passage efficiency of a Denil fish ladder on the Lamprey River in Newmarket, New Hampshire. The data collected allow for a better

understanding of the movements and diel behavior of river herring in fishways, as well as insight into how the selectivity of fish ladders my shape the population demographics within a river system.

A breached dam located at Wadleigh Falls on the Lamprey River in Lee, New Hampshire was examined to determine if river herring were able to pass the existing structure or if it should be considered the upper extent of their annual spawning migration. Telemetry data indicated that Alewives were unable to pass the breached Wadleigh Falls Dam site and that it should be considered the uppermost extent of their migratory access. Results also show that migrating fish arriving at the location had a strong preference for the river-right channel when migrating upriver and exhibited very little exploratory behavior to seek alternate pathways upriver before emigrating back downriver, approximately two weeks after river entry. These in-river residence times were very similar to those found in other telemetry studies of anadromous Alewives.

Successful management and effective stock assessment for any species requires an understanding of its reproduction and recruitment. Fecundity is one measure of the reproductive potential of a species and was assessed in this study. Mature adult Alewives were collected at the head-of-tide dam on the Lamprey River in Newmarket, New Hampshire during the vernal spawning migration in 2012. A gonadosomatic index was used to determine that fish were sampled before spawning occurred, and egg diameters were quantified to examine distribution of eggs throughout the ovary. Fecundity was estimated gravimetrically using two techniques for comparison, and no difference between the methods was found. These findings show that image analysis is a fast and reliable method for fecundity estimation that does not require the use of a commonly used, toxic solution for ovary preservation. Fecundity estimates using image analysis ranged from 147,400 eggs at 24 cm to 332,500 eggs at 34 cm and aligns with previous findings of a clinal trend along the Atlantic Coast. Fecundity increased with total length, somatic weight, and age. Simple linear regressions exhibited good fits for fecundity-total length and fecundity-somatic weight, with age being the best predictor.

INTRODUCTION

Species Background

Life history.**—**River herring, the collective name given to North American populations of Alewife (*Alosa pseudoharengus)* and Blueback Herring (*A. aestivalis)*, are anadromous members of the family Clupeidae with similar morphology, ecological roles, and overlapping distributions (Fay et al. 1983; Loesch 1987). Although similar in appearance, Alewife can be readily distinguished from Blueback Herring by differences in eye diameter, body depth, and peritoneum color (Bigelow and Schroeder 1953; Loesch 1987). Alewives are deeper bodied and have a larger diameter eye than that of Blueback Herring, generally exceeding the distance between the eye and snout. Peritoneum color of Alewives is described as pearly gray to pinkish white, whereas that of Blueback Herring is blackish or sooty (Collette and Klein-MacPhee 2002; Berlinsky et al. 2015). A distinction in the dorsal coloration of both species, grayish-green on Alewives and blue on Blueback Herring, was described by Bigelow and Schroeder (1953), but others found no detectable difference in coloration (MacLellan et al. 1981). Neves (1981) associated the greenish coloration of the Alewife with a deeper penetration of green light wavelengths in coastal waters and a deeper vertical distribution of Alewives (56 -110 m) relative to the Blueback Herring (27–55 m) while at sea. While not as readily assessed, other distinctions between the two species can be made with scale imbrication (MacLellan et al. 1981; Loesch 1987), otolith shape (Scott and Crossman 1973; Price 1978), genetic distinctions (Palkovacs et al. 2014; Berlinsky et al. 2015), and electrophoretic patterns of muscle myogen (McKenzie 1973).

Both species are similar in body size with maximum length 36–38 cm total length (Hildebrand and Schroeder 1928; Collette and Klein-MacPhee 2002), although few individuals exceed 30 cm (Ross 1991). Alewives are typically longer than Blueback Herring of the same age, and females of both species are generally longer and heavier than males of the same age (Fay et al. 1983; Loesch 1987). There is some evidence that a correlation exists between increasing latitude and an increased length at age for Blueback Herring (Richkus and DiNardo 1984). Both species are relatively short-lived with a maximum age of 11 years for Blueback Herring reported (Jessop 1993). Growth rates, age at sexual maturity, and longevity have been shown to vary greatly with geography (Collette and Klein-MacPhee 2002). Maturity and first spawning of river herring occurs between three and six years of age, with age four fish dominating virgin spawning fish and full recruitment to the spawning population by age five (Loesch 1987). As female river herring live longer than males, they tend to dominate the older age classes, whereas males are predominate in the younger age classes (Collette and Klein-MacPhee 2002).

Both species are sympatric throughout much of their distribution; Alewives are more common in northern waters along the Atlantic coast of North America ranging from Labrador and Newfoundland to South Carolina (Berry 1964; Winters et al. 1973; Burgess 1978; Collette and Klein-MacPhee 2002). Blueback herring are present as far north as Nova Scotia and Northeastern New Brunswick, but are the more abundant of the two species along the middle and South Atlantic coast, as far south as Florida, where Alewives are virtually non-existent (Bigelow and Schroeder 1953; Neves 1981; Alexander 1984; Collette and Klein-MacPhee 2002; McBride et al. 2010). Landlocked populations of both species are present in many freshwater lakes and man-made reservoirs including the Great Lakes and the Finger Lakes of New York (Bigelow and Schroeder 1953; Scott and Crossman 1973; Collette and Klein-MacPhee 2002).

Annual migration.—River herring spend most of their lives at sea, but as iteroparous (repeat spawning), anadromous fish they begin inshore migrations into freshwater to spawn annually once attaining maturity. Although some straying to adjacent streams likely occurs, available evidence suggests that river herring exhibit natal homing to their river of origin, possibly through olfactory clues (Belding 1920; Havey 1961; Thunberg 1971; Messieh 1977; Loesch 1987; Jessop 1994; Gahagan et al. 2012). The timing of spawning and associated migration is related to warming water temperature and therefore varies from south to north, but occurs within three to four weeks among years (Loesch 1987). Alewives generally begin their migrations when water temperatures reach approximately 5–10°C, while Blueback Herring prefer warmer temperatures (10 -15 °C; Belding 1920; Kissil 1969; Loesch 1987; Collette and Klein-MacPhee 2002). Loesch (1969) and Edsall (1970) found that both species ceased spawning activities when water temperatures exceeded 27 °C. As a result, within a year the presence of Blueback Herring is usually delayed by three to four weeks from the first observations of Alewives (Loesch 1987), but spawning peaks are only two to three weeks apart (Jones et al. 1978). Males of each species arrive earlier and in greater number than females each season (Collette and Klein-MacPhee 2002), likely related to the fact that they mature a year earlier (Havey 1961; Kissil 1974) and "ripen" earlier in the season (Cooper 1961). There is considerable overlap in the migration timing along the Atlantic seaboard, with mid-Atlantic, and northern most migrations (e.g., Gulf of Maine, Bay of Fundy, Gulf of St. Lawrence populations) migrating between March and early April and late April and mid-May, respectively. Spawning generally continues through July

(Rounsefell and Stringer 1945; Hildebrand et al. 1963; Kissil 1969; Marcy 1969; Tyus 1974; Loesch and Lund 1977; Loesch 1987; Scott and Scott 1988; Collette and Klein-MacPhee 2002).

Alewife and Blueback Herring exhibit distinct preferences of spawning habitats, and can be spatially isolated, even in streams and rivers with sympatry (Loesch 1987). Alewives prefer slower moving waters of ponds and coves as well as sluggish sections of streams above the head-of-tide (Collette and Klein-MacPhee 2002). Alewife spawning usually occurs over gravel, sand, detritus, and submerged vegetation in depths of 15 cm to 3m (Pardue 1983). In contrast, Blueback Herring tend to avoid the lentic sections of systems, instead seeking hard substrate to spawn where the flow is relatively swift (Collette and Klein-MacPhee 2002). When further upstream migration is barred by dams, as is the present situation in many coastal rivers, both species will spawn in close proximity, but Blueback Herring will spawn in the main stream flow while Alewife will spawn in shore-bank eddies or deep pools (Loesch and Lund 1977). Loesch (1987) described varying spawning site selection between Blueback Herring in the north (lotic) and south (lentic), and suggested it was done to reduce competition with Alewives in areas where the two species were sympatric. The adaptability of Blueback Herring to spawn in less-preferred, lentic environment of ponds in the north is also evident by the fact that they exist in Lake Champlain and successfully spawn in the head pond above the Mactaquac Dam on the Saint John River system (Loesch 1987).

The extent of upstream movement is often limited by man-made obstructions or natural barriers, but when accessible, appropriate spawning habitat determines the upstream distribution (Loesch and Lund 1977). Once arriving at the upper sections of spawning streams, spawning only lasts a few days for each wave of fish, followed by a rapid downstream movement into brackish or estuarine waters (Collette and Klein-MacPhee 2002). In the fall, adult river herring (ages 5+) move offshore and southward (Stone and Jessop 1992) where overwintering occurs in large schools of river herring of similar size comingled with other herring species. The presence, timing, and population structures of river herring have been well studied during the freshwater component of their life history, but much less so once they return offshore where they spend the majority of their lives (Lynch et al. 2015). Recent studies capitalizing on the advancement of genetic sampling and the presumed natal homing of river herring, have made advances in identifying the stock structure of river herring populations offshore, but more work needs to be conducted to fully understand population mixing (Palkovacs et al. 2014).

River herring are iteroparous and many individuals survive spawning and return in successive years. The amount of repeat spawning is highly variable and has been recorded in many systems (ASMFC 2012). Jessop et al. (1982) reported river systems where Alewife tended towards semelparity, as well as systems where individuals spawned up to seven or eight times. Richkus and DiNardo (1984) reported an average repeat spawning rate among populations of 30–40% and O'Neill (1980) found up to 75% repeat blueback spawning in Nova Scotia. However, other studies indicate that the amount of repeat spawning may exhibit a clinal trend, where northern Alewife populations (Nova Scotia) had as much as 60% repeat spawning, compared to only 10% in more southern populations (North Carolina).

Ecological role.—River herring play an important ecological role in both marine and freshwater ecosystems and provide an important trophic link between them. In freshwater systems, young of the year river herring are zooplanktivores feeding initially on rotifers (Crecco and Blake 1983), then primarily on cladocerans and copepods, beginning with relatively small species and progressing to larger species as they increase in size (Morsell and Norden 1968; Nigro and Ney 1982; Fay et al. 1983). Post et al. (2008) found that populations of anadromous Alewives were able to reshape the plankton community within spawning ponds. Prior to emigration, diets also include fish eggs, crustacean eggs, insects, insect eggs, and small fishes (Bigelow and Schroeder 1953). After emigration to the estuary and sea, Blueback Herring prey primarily on ctenophores, calanoid copepods, amphipods, mysids and other pelagic shrimps, and small fishes such as Atlantic Herring (*Clupea harengus*), Sand Lance (*Ammodytes americanus*), and Cunner (*Tautogolabrus adspersus*) (Collette and Klein-MacPhee 2002). Feeding behavior of Alewife at sea is very similar to that of Blueback Herring, however, some evidence suggests that Alewife and Blueback herring may utilize more particulate feeding, and filter feeding (Stone and Daborn 1987). Alewives also have diets more reliant on euphausiids than Blueback Herring in some regions (Stone and Jessop 1993; Bowman et al. 2000).

At all life stages, anadromous river herring are important forage for both freshwater and marine fishes (Moring and Mink 2002; Walter et al. 2003; Viverette et al. 2007). In the freshwater environment smaller adult river herring and juveniles are important prey species for Yellow Perch (*Perca flavescens*), White Perch (*Morone americana)*, Largemouth Bass (*Micropterus salmoides)*, Smallmouth Bass (*Micropterus dolomieu)*, and pickerel (*Esox* spp.) (Cooper 1961; Loesch 1987; Yako et al. 2000). In the marine environment, both species of river herring are important for a variety of predators including Spiny Dogfish (*Squalus acanthias*), Atlantic Cod (*Gadus morhua*), Silver Hake (*Merluccius bilinearis*), White Hake (*Urophycis tenuis*), Dusky Shark (*Carcharhinus obscurus*), Goosefish (*Lophius americanus*), Pollock (*Pollachius virens*), and Atlantic Halibut (*Hippoglossus hippoglossus*) (Rountree 1999; Bowman et al. 2000). Cooper (1961) and Tyus (1974) suggested that pelagic, schooling predators, such as Bluefish (*Pomatomus saltatrix*), Weakfish (*Cynoscion regalis*), and Striped Bass (*Morone saxatilis*), are more likely than solitary predators to use schooling clupeids like river herring as forage. Historically, when river herring populations were higher, it was suggested that large predators like Atlantic Cod were attracted inshore by river herring emigrations (Belding 1920; Ames and Lichter 2013). The loss of the nutritious and predictable food source that river herring supplied has been suggested as an association to the decline in coastal Atlantic Cod populations (Baird 1883; Ames 2004; Hall et al. 2011). In addition, birds, amphibians, reptiles, and mammals have also been identified as predators consuming river herring as part of their diet (Loesch 1987).

Like Pacific salmon species, river herring act as vectors of transport for marine-derived nutrients to freshwater ecosystems (Browder and Garman 1994; Walters et al. 2009). Durbin et al. (1979) concluded that anadromous Alewives transport P, N, C to a freshwater system over a two month period comparable to salmon migrations in Alaska. Marine derived organic matter from Alewife carcasses, gametes, and excretion has been shown to be incorporated into stream invertebrates and piscivorous fishes (Garman and Macko 1998; Post and Walters 2009). These marine-derived nutrients often serve as critical additions of energy and nutrients, which are vital to food webs, even beyond the lakes and streams where anadromous species spawn (Limburg and Waldman 2009). West et al. (2010) concluded that when spawning populations were small, and juvenile survival was high in a system, migrating Alewives resulted in a net export of phosphorous. With high adult populations and poor juvenile survival, however, a net import of nutrients can occur. Sedimentation rates of lakes can also be reduced with increased leaf litter decomposition in response to microbial stimulation provided by Alewife mortality in the system (Durbin et al. 1979).

Fishery and population decline **—** River herring supported one of the oldest documented fisheries in North America, with some records as far back as 350 years (Kocik 1998; NOAA

2009). Subsistence fisheries harvesting river herring began as early as the 1700s in New England (Spencer 2009). The earliest consistent records of U.S. commercial landings of river herring were from Maryland, North Carolina, Virginia, and Massachusetts for the time period between 1887 and 1928, when average annual domestic landings were estimated at 18.5 million pounds (ASMFC 2012). Harvested river herring have historically been used for bait, food, fish meal, fish oil, and fertilizer, although their scales briefly commanded a high price for use in the manufacture of artificial pearls around the time of World War I (Scott and Scott 1988; Collette and Klein-MacPhee 2002). Coast wide landings of river herring remained relatively stable through the 1940s, increased sharply in the 1950s, peaked at 74.9 million pounds in 1958, remained high through the early 1970's as fleets from other countries entered the US inshore fishery, and began declining in the late 1970's to only a fraction of peak levels (NOAA 2009; ASMFC 2012). Alewife and Blueback Herring are still targeted today, and incidentally caught as bycatch, in a number of different fisheries by both commercial and recreational fishermen (Bethoney et al. 2013; Cournane et al. 2013; Bethoney et al. 2014a, 2014b). Recreational anglers use small weirs, cast nets, dip nets, seines, or hook and line to capture river herring for primary use as bait for sportfish such as Striped Bass and Atlantic Cod.

Recent estimates of both species of river herring suggest they presently occur at ≤1% of their historic population levels (Haas-Castro 2006; Limburg and Waldman 2009; ASMFC 2012). Natal homing of Alewife and Blueback Herring has led to many small, geographically distinct populations. As a result of prolonged depletion, the Atlantic States marine Fisheries Commission (ASMFC) established a management plan for river herring in 1985 that established mechanisms to regulate harvest, increase access to spawning habitat, and restore populations through stocking efforts (ASMFC 2012). Despite these efforts, minimal population recoveries have led to a listing river herring as a "species of concern" by the National Oceanic and Atmospheric Administration's (NOAA) Fisheries Service in 2006 (NOAA 2009). At the time of the listing, Massachusetts, Rhode Island, New York, and North Carolina voluntarily closed their state fishery for river herring. In 2012 the Atlantic States Marine Fisheries Commission passed Amendment 2 to the fisheries management plan that required states to close commercial and recreational fisheries in their state waters unless they could provide a sustainable fishery plan. The ASMFC approved plans for Maine, New Hampshire, New York, North Carolina, and South Carolina to allow those fisheries to continue. The lack of recovery following NOAA's listing warranted further consideration of river herring as candidates for threatened or endangered species listing under the U.S. Endangered Species Act (NOAA 2013). While the exact cause(s) of this population decline are unknown, the most likely threats include loss of spawning habitat due to dam construction and other impediments to migration, habitat degradation, fishing pressure, and increased predation due to recovering Striped Bass populations (ASMFC 2012).

Dams and Fish Ladders

Land development and dam construction have significantly impacted river herring populations directly by limiting their access to historic spawning sites (Saunders et al. 2006; Hall et al. 2011; Lynch et al. 2014) and indirectly by changing the ecology of rivers; causing alterations in water temperatures, sediment and nutrient retention, flooding, and resident freshwater fish communities (Limburg and Waldman 2009). The habitat and population loss resulting from dams leads to alterations in existing food webs, loss of biodiversity, species decline, and ultimately extirpation (Hall et al. 2011).

In the northeast, dams are seen as the primary cause of declines by blocking access to large portions of historical spawning grounds (Belding 1920; Limburg and Waldman 2009; Hall et al. 2011; Hall et al. 2012). In New Hampshire, the Merrimack, Lamprey, Cocheco, Oyster, Taylor , Exeter, and Salmon Falls Rivers currently have dams at, or near, the head-of-tide and have had had them in place for more than a century, suggesting levels of habitat loss and associated river herring population reductions.

A common technique to reopen interconnected waterways has been the installation of fish ladders at dams on coastal rivers. Many types of technical fish ladders have been constructed with a common goal of allowing fish to pass above dams as quickly as possible with a minimal amount of stress, injury, delay, or mortality (Franklin et al. 2012). However, even in a well-designed fishway the passage is often species-specific and the number of fish able to pass is far below that which would pass in the absence of the dam (Limburg and Waldman 2009). Denil and Alaska steeppass fishways are common examples of baffle-type fishways that were originally constructed at dams for salmonids, but have been extensively used in rivers where river herring are now the primary species of interest for passage (Haro et al. 1999). Despite their widespread use, the efficacy of anadromous clupeid passage, including that of Alewife and Blueback Herring, has rarely been evaluated, and results from limited studies have varied widely (Castro-Santos and Vono 2013).

Tagging Studies and PIT Tags

A passive integrated transponder (PIT) tag is an electronic microchip encased in glass and available in various lengths and diameters (Gibbons and Andrews 2004). PIT tags can be coded with a unique number that can be assigned to a captured individual. The tags are “passive” in that they do not contain a power source, but rather remain dormant until being activated by a stationary or hand held reader. The reader generates a close-range electromagnetic field that energizes the tag long enough to transmit its unique number. The tags are usually inserted under the skin of an individual, in the stomach, or surgically implanted in the body cavity (Gibbons and Andrews 2004).

A primary benefit of PIT tags in fisheries research is the ability to repeatedly collect information from individuals throughout their life, without visually observing or physically recapturing them. A disadvantage of PIT tags is the relatively short detection range compared to other active transmitters, but this makes them well suited for application in studying movements in confined spaces such as culverts and fish ladders. The short detection range in these confined spaces decreases the overlap of tagged individuals and allows for more precise detection (Castro-Santos Vono 2013).

The earliest studies using PIT tags examined fish movements (Prentice and Park 1983) and have since been used on many fish species as well as on mammals, amphibians, reptiles, birds, and invertebrates. The value of PIT tags in assessing alosines and fish ladders has been realized in recent years with studies to measure the tagging effects on these species and to quantify their movements (Castro-Santos et al. 1996; Haro et al. 1999; Bunt et al. 2012; Franklin et al. 2012; Castro-Santos and Vono 2013).

Fecundity

Fecundity estimates are important in fisheries management to determine the reproductive potential of fish in a population, and can be used to predict trends in species abundance and as a measure of the spawning stock biomass (Nitschke et al. 2001). Reproductive metrics can be correlated with abiotic factors, such as temperature, and incorporated in stock assessment models (Murua and Saborido-Rey 2003). Differences in fecundity exist among and within species and often among different geographic stocks, and individual fish depending on their size and age (Bagenal 1978). In heavily exploited fish populations, particularly those at low abundance levels like river herring, large, old fish will be eliminated more rapidly because they are more susceptible to size-selective fishing mortality (Trippel 1999). Changes in population dynamics including the loss of older, experienced spawning fish, and smaller sizes (ages) at maturity are often indicators of populations under stress. Highly fecund species are better adapted to reestablishment after population reductions or extirpation due to pressures, such as overfishing, environmental changes or habitat loss.

Alewife and Blueback Herring are both highly fecund species, but all of the fully developed oocytes may not be ovulated during a spawning season (Jessop 1993). Previous river herring fecundity estimates range from 100,000 to 450,000 and 30,000 to 400,000 eggs in Alewife and Blueback Herring, respectively (PSEG 1984). Jessop (1993) demonstrated that reproductive parameters vary by latitude, with northern stocks of both species having lower gonadosomatic indices (ovary/total body weight), lower fecundity, higher egg weight, and more complete gamete development prior to river entry.

CHAPTER 1

USING PASSIVE INTEGRATED TRANSPONDER TAGS TO DETERMINE THE EFFICACY OF A STANDARD DENIL FISHWAY FOR ALEWIFE (*ALOSA PSEUDOHARENGUS*) PASSAGE

Introduction

Dams were constructed for harnessing mechanical energy during the textile and industrial boom along the east coast, and are still in use for electrical generation. Land development and dam construction have significantly impacted river herring populations as well as other diadromous species by directly limiting their access to historic spawning sites (Saunders et al. 2006; Hall et al. 2011; Lynch et al. 2014). Dams also negatively impact fish populations by changing the ecology of rivers, e.g. causing alterations in water temperatures, increasing sediment and nutrient retention, more frequent flooding, and changes in the resident freshwater fish communities (Limburg and Waldman 2009). The habitat and population loss resulting from dams leads to alterations in existing food webs, loss of biodiversity, species decline, and ultimately extirpation (Saunders et al. 2006; Hall et al. 2011; Lynch et al. 2015).

River herring, the collective name given to North American populations of Alewife and Blueback Herring, are iteroparous, anadromous members of the family Clupeidae with similar morphology, ecological roles, and overlapping distributions (Fay et al. 1983; Loesch 1987).

Alewives are more common in northern waters along the Atlantic coast of North America (Winters et al. 1973; Burgess 1978; Collette and Klein-MacPhee 2002), whereas Blueback Herring are more abundant along the middle and south Atlantic coasts, as far south as Florida (Bigelow and Schroeder 1953; Neves 1981; Collette and Klein-MacPhee 2002; McBride et al. 2010). Both species have a maximum total length of ~36–38 cm (Hildebrand and Schroeder 1928; Collette and Klein-MacPhee 2002; Ross 1991) and are relatively short-lived (maximum age ~11 years) (Jessop 1993). River herring spend most of their lives at sea, but begin inshore migrations into freshwater to spawn annually once attaining maturity between three and six years of age (Loesch 1987).

Recently, many species of diadromous fish have exhibited large scale declines in North America. River herring are believed to only be present at 1% or less of their historic population levels (Haas-Castro 2006; Limburg and Waldman 2009; ASMFC 2012), and were listed as a "species of concern" by the National Oceanic and Atmospheric Administration's (NOAA) Fisheries Service in 2006 (NOAA 2009). Exact causes of the decline are unknown, but fishing pressure, habitat degradation, increased predation due to recovering striped bass populations, and loss of habitat due to the construction of dams are all likely (ASMFC 2012).

Dams, which block access to large portions of historical spawning grounds, are seen as the primary cause of river herring declines in the Northeast (Belding 1920; Limburg and Waldman 2009; Hall et al. 2011; Hall et al. 2012). It has been shown that river herring can rapidly (3-5 yrs.) repopulate rivers if afforded access above dams through fishways (Pardue 1983; Lichter et al 2006; Hall et al. 2011). A common technique to reopen interconnected waterways has been the installation of fish ladders at dams on coastal rivers. Many types of technical fish ladders have been constructed with a common goal of allowing fish to pass above dams quickly, with a minimal amount of stress, injury, or mortality (Franklin et al. 2012). However, even in a well-designed fishway the passage is often species-specific and the number of fish able to pass is far below that which would pass in the absence of the dam (Limburg and Waldman 2009). Denil and Alaska steeppass fishways are both examples of baffle-type fishways that were originally constructed at dams for salmonids, but have been extensively used in rivers where river herring are now the primary species of interest for passage (Haro et al. 1999). Their relatively inexpensive construction and maintenance costs, and their ability to operate at low head dams with a wide range of natural discharge rates, often leads to their selection. Despite their widespread use, efficacy of anadromous clupeid passage, including that of Alewife and Blueback Herring, has rarely been evaluated, and results from limited studies have varied widely (Castro-Santos and Vono 2013).

The current study was undertaken to estimate the efficacy and selectivity of technical fishways for passage of river herring. Fishways have become a primary source of the data used to estimate population size (ASMFC 2012), thus examination of the selectivity effects of fishways can help provide insight to how they shape population structures (e.g., absence of smaller fish).

Methods

Study area

The passage efficiency, movement, and diel behavior of Alewives were quantified at a simple Denil technical fishway using PIT telemetry (Castro-Santos et al. 1996) over three consecutive spring (April–June) spawning runs between 2013 and 2015. The study was conducted on the Lamprey River, a major tributary to Great Bay Estuary. Its headwaters are in

Northwood, NH, and it flows approximately 80 km south and east until entering the Great Bay Estuary in Newmarket, NH. The fishway is located at Macallen Dam situated at the head-of-tide at river kilometer (rkm) 3.0, in Newmarket, NH (Figure 1.1). The dam, constructed in 1887, is a low head dam, 8.2 m high, with a spillway width of 45.7 m. The fishway is a standard Denil type technical fishway constructed in 1972 by the New Hampshire Fish and Game Department for restoration efforts of diadromous species. The fishway is 52.7 m long with a 180 degree turn at 21.9 m, an elevation of 6.9 m, a width of 0.9 m, and a 1:6 slope. It is constructed with alternating sloped and flat sections (resting pools) with a 3.7 x 4.0 m trap area after the uppermost sloped section. Fish passage through the ladder is monitored daily by New Hampshire Department of Fish and Game. The mean annual river herring run at the fishway over the past two decades was 46,275 fish, but has exhibited large increases in recent years with highest passage of 86,862 fish in 2012. It is also usually the largest single-river run in New Hampshire each year. As part of river herring restoration efforts, the fishway is operated each spring from April through the end of June. A 20.32 cm Smith Root electronic counting tube is installed in the trap to continually allow fish to pass into the river above the dam. Daily visits are made to ensure correct operation of the fishway and Smith Root electronic counting equipment. As it is only possible for a few fish to pass through the single counting tube simultaneously, the number of fish entering the fishway exceeds the passage rate through the counting tube during the periods of peak river herring abundance. Therefore, fish are also passed daily by net during those periods of high activity to maximize annual passage through the fishway.

Antennas

To detect PIT tags, eight antennas were constructed. Each had three turns of 12 gauge thermoplastic high-heat-resistant nylon insulated copper wire, placed inside 1.27 cm polyvinyl chloride tubing for mechanical protection. An antenna was fixed to the baffle on each end of the three resting pools (6 antennas), one was fixed to the entrance of the fishway, and one was fixed to the last baffle before the trap at the top of the fishway (Figure 1.2; Figure 1.3).

Each antenna was tuned to resonate at 132.4 kilohertz and was attached, with twin-axial cable, to a multireader board of eight Texas Instruments Radio Frequency Identification Systems designed by research ecologists from the United States Geological Survey Conte Anadromous Fish Research Center. The multireader was housed in the basement of a building adjacent to the fishway in 2013, and was housed in a weatherproof box at the top of the fishway in 2014 and 2015 (Figure 1.4). In all years, the multireader setup included a laptop computer to log PIT detections, a backup power supply, and a DC regulated power supply connected to an AC power source. The laptop computer logging the data was connected wirelessly to the internet, allowing

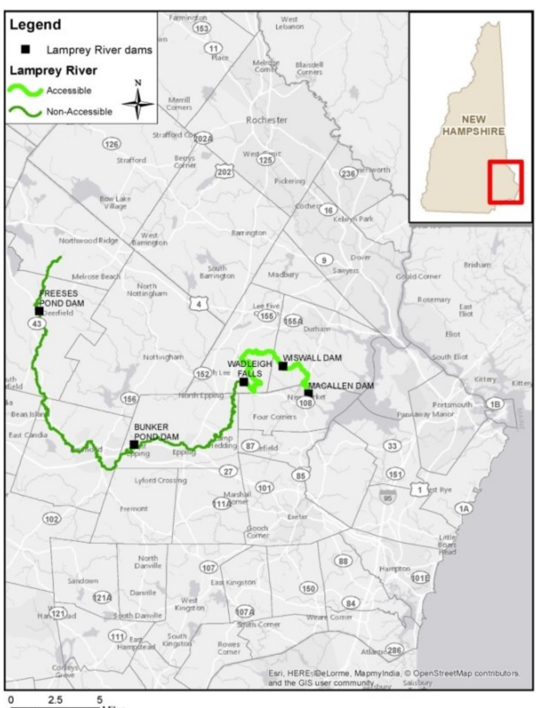

FIGURE 1.1.—Map of the Lamprey River, New Hampshire showing dam locations and accessible freshwater habitat.

FIGURE 1.2.—Loop antenna contained within PVC housing and mounted to wooden baffles placed within the fishway.

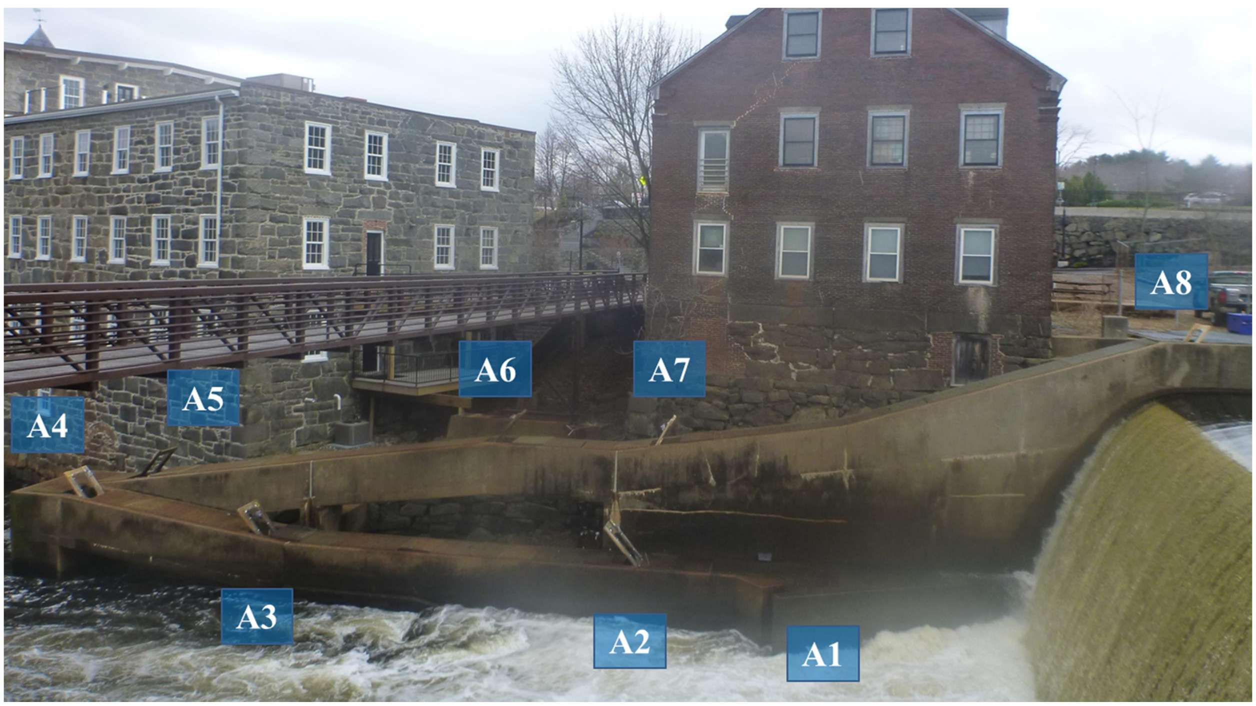

FIGURE 1.3.—Denil fishway at head-of-tide Macallen Dam on the Lamprey River in Newmarket, New Hampshire. The location and number of each PIT antenna are shown and baffles raised to show location within fishway.

remote control of the computer and multireader system, the ability to ensure its correct operation from a remote location, and downloading of data on a regular basis. Antenna number, fish identification number, date, and time of each tag detection was recorded by the computer in a text file. Proper operation of all antennas was checked at least once a week by lowering a "marker" tag into the reading plane of the antenna from above. A marker tag was also permanently attached to the baffle holding the uppermost antenna of the array and was set to transmit at 30 minute intervals throughout the study period to ensure continuous monitoring by the multireader. During periods of high activity within the fishway, potential exists that more than one fish will be simultaneously in the detection field of an antenna, leading to a possibility of missed detections due to signal collision. Similarly, missed detections would occur if a tagged fish passed by an antenna too quickly, entering and exiting the detection field between antenna reading intervals. To account for this, a single antenna reader efficiency was calculated for each year. This was done by dividing the total number of fish known to have passed a particular antenna (by detection at an antenna above or below it in the array depending on the direction of travel), by the total number of fish that were actually detected by that antenna. Using a single fish as an example, if it was detected at antennas 1, 2, 3, 5, 6, and 8, that would mean that it was missed by antennas 4 and 7, so of the 8 possible detections (at antennas 1 through 8) it was detected only 6 times, for a reader efficiency of 75%. The single annual value was based on all fish detections by all antennas.

Fish tagging

Adult river herring were collected using two methods. The first entailed capturing fish within a 100 m radius of the fishway entrance using a 1.22 m diameter X 0.635 cm mesh cast net, in approximately 1.5 m of water at low tide. This method was preferred and used whenever fish were abundant in the area below the fishway. The second method employed a weir located approximately 400 m downriver of the fishway, and was used in 2013 only. The weir was emptied daily and collected fish were removed and tagged immediately. Fish that appeared to be healthy in swimming activity and appearance (e.g. minimal scale loss) were measured to the nearest millimeter, sex recorded and tagged, as below. Fish exhibiting abnormal swimming behavior or in compromised health were not used. To insert the tag, a small incision (~ 5 mm), was made between two rib bones immediately above the right pelvic fin, and a uniquely coded 23 mm HDX PIT tag (3.65 mm X 23.0 mm; 0.6 g air weight) was inserted into the body cavity through the incision (Figure 1.5). Once the tag entered the body cavity, the incision was sealed with Vetbond tissue adhesive (3M) and allowed to harden for eight seconds. The tagging process typically took less than 30 seconds.

FIGURE 1.4.—PIT antenna reader setup used for monitoring Macallen Fishway. Top left: equipment housed in basement of adjacent building in 2013; Bottom left: Two weather proof boxes placed at the top of the fishway were used in 2014 and 2015; Right: multireader board containing 8 RFID readers, port replicator, and laptop computer.

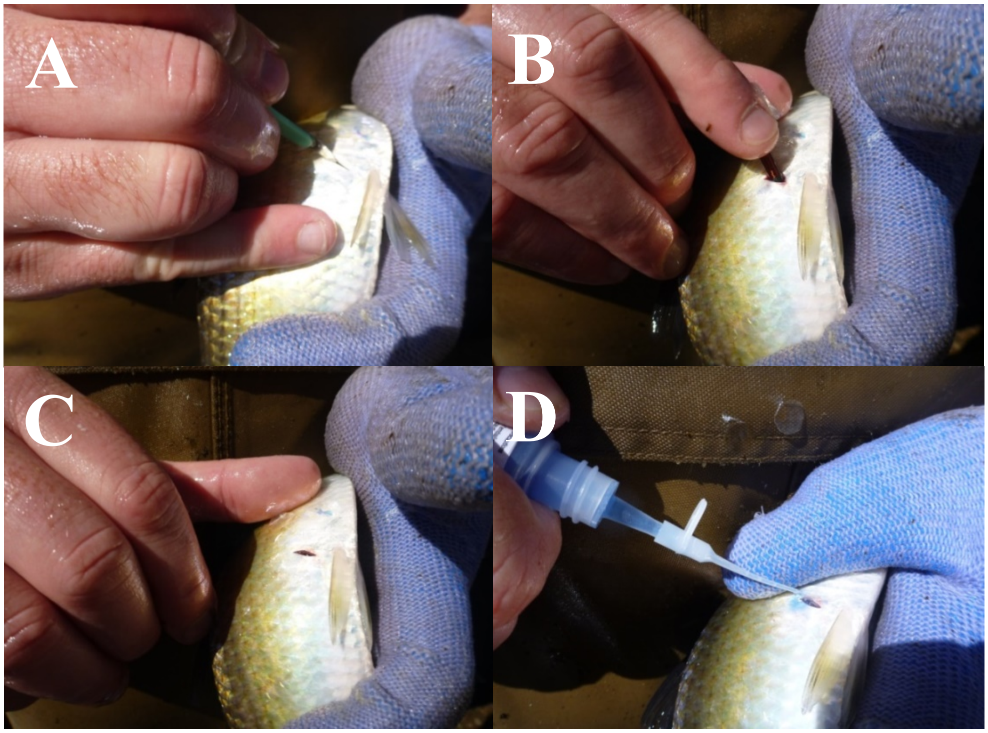

FIGURE 1.5.—Alewife tagging with 23mm PIT tags. A) approximate 5 mm incision made just above the insertion of right pelvic fin; B) PIT tag inserted into body cavity; C) incision after tag insertion; D) Vetbond adhesive applied to seal incision.

Following tagging, fish were placed in a 113.5 liter recovery tank containing river water and observed for about five minutes before being returned to the river at the site of capture. If a fish exhibited physical or behavioral distress (e.g. lethargic or erratic swimming, scale loss, discoloration, labored respiration) it was recorded and excluded from analysis.

Data processing and metrics

During data processing of PIT records, successive detections of an individual fish were grouped into single "presences" for analysis. A presence was defined as a single or sustained detection of a fish at the same antenna, where the duration of that presence was the difference between the first and last detections at that antenna. If there was a gap of one minute or more between detections at an antenna (< 0.03% of detections) then the detection after that period was identified as a new presence at the same antenna. Two consecutive presences at different antennas, whether adjacent or not, were considered a movement. Movements were classified as entries into the fishway or movement either upward or downward, and the duration of the movement was the difference between the first detection of a presence and the last detection of the previous presence. The location of the lowermost antenna (A1; Figure 2) at the entrance to the fishway allowed for detection of fish that were in close proximity to the fishway, but did not necessarily enter the fishway. Therefore, at least a single presence at antenna 2 was used to classify a fish as having entered the fishway. A single attempt by a tagged fish was initiated upon first entering the fishway and continued until a fish was recorded exiting the fishway, regardless of how long the individual spent within the fishway. A fish was determined to have exited if it was detected for two consecutive presences at antenna 1 with a lag of at least 15 minutes between detections. If a fish ascended the fishway to the top and then volitionally descended to antenna 1 before immediately ascending the fishway again, this was only counted as a single attempt as the fish did not exit the fishway. A fish was classified as having ascended to the top of the fishway when detected at the uppermost antenna (A8; Figure 2) and was classified as passing if the last detection during the season was also at that antenna.

Alewives were sampled each year at the study site to obtain lengths and scale samples for aging. The von Bertalanffy growth equation (von Bertalanffy 1938) was applied to the length-age data to predict the age of each fish when tagged, and that predicted age was advanced by one year for each monitoring season to predict the length of a tagged fish in successive years. Means comparisons were conducted for various factors of fish passage and movement within the fishway using Welch's t-tests incorporating a Satterthwaite approximation to account for possible differences in sample variances from unequal sample sizes. Binomial logistic regressions were conducted to measure the effects of total length, sex, sampling week, and tagging stress on probability of attraction to the fishway, ascending to the top of the fishway ($R_{success}$), and passage ($P_{success}$). Attraction was defined as the ability of a fish to locate and follow the fishway entrance flow amongst the other flows and turbulences present at the base of the dam. Models were run stepwise with a full model and non-significant variables (at $P \leq 0.10$) were removed until the model with lowest AIC value was selected.

Results

Tagging

In 2013, 621 Alewives (212–332 mm TL; mean = 283 mm TL; SD = 20.7) were collected and tagged on seven dates between April 26 and May 31, 2013. In 2014, 501 Alewives (236–351 mm TL; mean = 289 mm TL; SD = 19.8) were collected and tagged on six dates between May 3 and June 4, 2014. No fish were tagged in 2015 (Table 1.1). Most fish were collected immediately below the fishway, but collections from the weir ($N = 120$) were required for the last two weeks in 2013, when Alewife were not present in sufficient abundance to be cast netted. Forty nine (49) Blueback Herring were collected and tagged, but were excluded from all analyses because very few (3 fish) attempted to enter the fishway and none passed.

Antenna monitoring

Antenna arrays were operational and monitored continuously for 47 days (April 26 –May 7) in 2013, 56 days (April 25–June 20) in 2014, and 58 days (April 27–June 24) in 2015. There was only a single monitoring interruption of 4.7 hours on May 7, 2013 as a result of a computer update. In 2013, antennas made 1,673,419 detections of 130 tagged fish over 14 days. Individual detections were grouped into 3,515 movements of Alewives into the fishway or up

TABLE 1.1.—Number of Alewives tagged, mean lengths, and number detected at Macallen Dam fishway.

Tagging date	N	Number (%) of males	Total length (cm)	Number (%) detected 2013	2014	2015	All years
2013							
April 26	251	134 (53.4)	293.12 ± 17.44		91 (36.3)	28 (11.2)	91 (36.3)
May 1	200	112 (56.0)	281.67 ± 17.73	124 (62.0)	98 (49.0)	25 (12.5)	161 (80.5)
May 7	17	7 (41.2)	268.35 ± 13.96	5 (29.4)	8 (47.1)	1 (5.9)	12 (70.6)
May 8	33	17 (51.5)	272.85 ± 17.31	1 (3.0)	11 (33.3)	6 (18.2)	12 (36.4)
May 13	50	33 (66.0)	269.06 ± 21.48	1 (2.0)	15 (30.0)	4 (8.0)	15 (30.0)
May 17	21	16 (76.2)	278.48 ± 15.62	0 (0.0)	4 (19.0)	0 (0.0)	4 (19.0)
May 31	49	44 (89.8)	262.55 ± 21.68	0 (0.0)	9 (18.4)	3 (6.1)	11 (22.4)
2014							
May 3	198	105 (53.0)	295.34 ± 14.67		176 (88.9)	48 (24.2)	178 (89.9)
May 6	149	98 (65.8)	299.91 ± 15.25		107 (71.8)	38 (25.5)	115 (77.2)
May 12	50	25 (50.0)	275.84 ± 15.77		23 (46.0)	11 (22.0)	28 (56.0)
May 16	50	22 (44.0)	272.44 ± 14.93		6 (12.0)	18 (36.0)	23 (46.0)
May 30	49	22 (44.9)	266.31 ± 15.08		6 (12.2)	19 (38.8)	23 (46.9)
June 4	6	5 (83.3)	244.33 ± 7.23		0 (0.0)	1 (16.7)	1 (16.7)

TABLE 1.2.—Monitoring periods, count of detections, movements, and reader efficiency of antenna array.

Monitoring dates	Days	Hours	Hours missed	Detections recorded	Antenna reader efficiency	Number of fish detected	Days of movements	Number of movements
2013								
April 29 - June 12	44	1,057	4.7	1,673,419	99.55%	130	16	3,516
2014								
April 25 - June 20	56	1,341	0	8,832,430	99.04%	552	33	10,714
2015								
April 27 - June 24	58	1,390	0	3,423,022	96.50%	202	21	4,534

and down between antennas (Table 1.2). Detections (8,832,430) were recorded on 33 days in 2014 classifying, 10,714 movements of 509 fish within the fishway. In 2015, no fish were tagged, but antennas recorded 3,423,022 detections of 202 fish tagged in prior years, classifying 4,534 movements within the fishway over 21 days. Reader efficiency was high in all years, ranging from 96.50% in 2015 to 99.55% in 2013. Most instances of fish at non-consecutive antennas were a result of fish missed moving both up and down between antennas A1 and A2. This was likely due to signal collision, as fish congregate in that section which is flooded at higher tide stages. The 4.7 hour interruption in monitoring that occurred in 2013 was responsible for most non-consecutive detections at higher antennas.

Fishway attraction

Fishway attraction was assessed in 2013 and 2014 using only fish tagged within each year. Due to conflicts between tag type and reader software in 2013, only 370 of the 621 tagged fish were used in the analysis for attraction. All fish tagged (N = 370 in 2013; N = 501 in 2014) were assumed to be available for attraction to the fishway. One hundred and twenty three of the 370 fish tagged in 2013 and 284 of 501 fish tagged in 2014 entered the fishway, for attraction rates of 33% and 57% respectively (Table 1.3). More males entered the fishway in both years, but logistic regression analysis indicated sex was not a factor in determining attraction success in either year (Table 1.4). Total lengths of fish attracted to the fishway for both years ranged between 240 and 330 mm (mean = 292 mm; SD = 18.0) and were significantly larger than fish that were unable to find the fishway (mean = 276 mm; SD = 20.2; t = 12.41; P < 0.001; df = 868.8; Table 1.5). Logistic regressions were conducted for each year and for both years combined to estimate the likelihood of a fish being attracted to the entrance to the fishway ($A_{success}$). Analysis with length, sex, and sample week as explanatory variables showed that the number of weeks a fish was tagged after fish first appeared at the fishway was a significant factor in both years and total length was significant in 2013 (z = 2.637; P = 0.008; Table 1.4; Figure 1.6). Model results for a 285 mm fish (mean length of fish returning to fishway 2013–2015) had a 61% probability of attraction if present in the first two weeks and 13% if in the weeks following (Figure 1.6).

Fishway ascension and passage

Cumulative ascension success within the fishway each year was high (≥ 82%) through the first resting pool (A4) and dropped to 69%–80% at the second resting pool (A6). Successful ascension to the top of the fishway was lowest in 2013 (64%) but higher at similar levels in 2014 and 2015 (77% and 78% respectively; Table 1.3). The number of ascension attempts by a fish ranged from 1 to 19 with a median of two attempts in all years. No differences in number of attempts were found between sexes for all years. In 2013, fish that successfully ascended the fishway made significantly more attempts than those that did not succeed, but that difference was not found in other years (Table 1.5). Fish successfully ascending to the top of the fishway were significantly larger than those that did not for all years of the study (t = -7.24; P < 0.001; df = 551; Table 1.5). The transit time of fish ascending to the top of the fishway was highly variable, with a minimum and maximum of 18 minutes and 89 hours, respectively (3.3–17.2 hour median times; Table 1.3). There was agreement between transit times of males and females within each year, with means between 14.1 and 14.8 hours (Table 1.4). Logistic regression analyses for each year individually and for all years combined were conducted to determine likelihoods of success in ascending to the top of the fishway ($R_{success}$) with total length, sex, sample week, and year tagged as explanatory variables. Sample week and sex were not factors in predicting $R_{success}$ in all years (Table 1.6). The number of years since tagging was significant (z = 3.550; P < 0.001) in 2014, when fish tagged in 2013 and 2014 both returned. In 2015 when all fish were tagged at least one year prior there was agreement among groups by years since tagging. Total length was a significant predictor of $R_{success}$ in both 2013 (z = 4.467; P < 0.001) and 2014 (z = 4.336; P < 0.001), but not in 2015, when all fish included in the analysis had at least one additional year of growth, thus the smallest size fish in 2013 and 2014 analysis would no longer be present. As years since tagging (within year vs. prior) in 2014 significantly reduced likelihood of fishway attraction and ascension, the final model to predict $R_{success}$ only includes fish that were tagged at least one year prior. Total length, sex, and years since tagging were all considered as explanatory variables in the final model, but only total length was significant (z = 2.119; P = 0.034; Table 1.6; Figure 1.7). Final model results for a 285 mm fish (mean length of fish returning to fishway 2013–2015) had a 74% probability of ascending to the top of the fishway (Figure 1.6).

Logistic regression analyses of $P_{success}$ were very similar to those for $R_{success}$. Sample week and sex were not factors in predicting $P_{success}$ in all years (Table 1.7). The number of years since tagging was significant (z = 3.637; P < 0.001) in 2014 when returning fish tagged in 2013 and fish tagged in 2014 were both present. In 2015 when all fish were tagged at least one year prior there was agreement between groups by years since tagging. Total length was a significant predictor of $P_{success}$ in both 2013 (z = 3.722; P < 0.001) and 2014 (z = 4.200; P < 0.001), but not in 2015. As with $R_{success}$ years since tagging in 2014 significantly reduced likelihood of fishway attraction and ascension, the final model of $P_{success}$ only includes fish that were tagged at least one year prior. Total length, sex, and years since tagging were all considered explanatory variables in the final model, but only total length was significant (z = 2.286; P = 0.022; Table

TABLE 1.3.—Summary data for attraction, ascension, attempts, and passage analysis for all three monitored years (2013–2015).

	2013	2014	2015
Fish tagged in year:	621	501	-
Total fish tagged to date:	621	1,122	1,122
Number of fish detected:	130	552	202
		Attraction analysis	
N:	370	501	-
Number (%) attracted:	123 (33%)	284 (57%)	-
Mean (±SD) total length:	284 (± 18.7)	295 (± 16.5)	-
Male / female:	63 / 60	165 / 119	
Median time (hours) after tagging:	78.5	95.7	
		Ascended to top of fishway	
N:	79	392	155
% of fish attracted to fishway:	64%	77%	78%
Mean (±SD) total length[a]:	289 (± 18.2)	299 (± 15.2)	306 (± 17.5)
Male / female:	36 / 43	224 / 168	81 / 74
Median transit time (hours):	5.6	17.2	3.3
Number of times ascended to top:			
1	66	361	143
2	11	29	11
3	2	2	1
Median time (hours) in trap before descent:	2.9	6	15.9
		Attempts	
Maximum attempts by a single fish:	19	17	18
Mean (SD):	3.5	3	3.6
Median:	2	2	2
		Passage	
N:	46	346	131
% of fish attracted to fishway:	37%	68%	66%
% of fish ascending fishway:	58%	88%	85%
Male / female:	21 / 25	201 / 145	67 / 64
Mean (±SD) total length:	292 (± 18.1)	298 (± 14.6)	306 (± 17.6)
		Cumulative ascent	
Ascend to A2:	95%	92%	98%
Ascend to A3:	85%	91%	97%
Ascend to A4:	82%	90%	96%
Ascend to A5:	77%	79%	88%
Ascend to A6:	69%	73%	80%
Ascend to A7:	62%	72%	77%
Ascend to A8:	61%	71%	76%

[a] *Total lengths are predicted for years since tagging using the equation* $L_t = L_\infty(1-e^{-k(t-t0)})$ *(von Bertalanffy 1938).*

TABLE 1.4.—Logistic regression analysis results for probability of attraction success ($A_{success}$). Best models (ΔAIC ≤ 2) are shown in bold. TL = total length, SW = sample week.

Logistic regression model	Significant variables	Significance	AIC	ΔAIC
		2013		
logit($A_{success}$) = 0.03*TL - 4.58*SW -7.91	**TL, SW**	**TL(z = 3.749; P < 0.001) SW(z = -4.516; P < 0.001)**	**348.95**	**-**
logit($A_{success}$) = 0.03*TL - 0.26*Sex - 4.63*SW - 9.02	**TL, SW**	**TL(z = -2.158; P = 0.028) SW(z = -4.553; P < 0.001)**	**350.17**	**1.22**
logit($A_{success}$) = 0.03*TL - 4.26*Sex - 10.37*SW + 0.02*TL:Sex - 0.03*TL:SW + 18.44*Sex:SW - 7.20	TL	TL(z = -2.158; P = 0.028)	356.16	7.21
logit($A_{success}$) = -4.73*SW -7.91	SW	SW(z = -4.731; P < 0.001)	362.00	13.05
		2014		
logit($A_{success}$) = 0.01*TL - 2.46*SW - 1.46	**SW**	**SW(z = -8.178; P < 0.001)**	**537.10**	**-**
logit($A_{success}$) = 1.08 - 2.68*SW	**SW**	**SW(z = -10.800; P < 0.001)**	**537.61**	**0.51**
logit($A_{success}$) = 0.01*TL - 0.18*Sex - 2.39*SW - 2.19	**SW**	**SW(z = -7.621; P < 0.001)**	**538.51**	**1.41**
logit($A_{success}$) = 0.25 + TL - 4.27*Sex - 5.82*SW + 0.01*TL:Sex - 0.01*TL:SW + 6.97*Sex:SW			545.70	8.60
		Final (all years)		
logit($A_{success}$) = 0.02*TL - 4.37*Sex + 2.61*SW + 0.02*TL:Sex - 0.02*TL:SW + 5.28*Sex:SW - 6.75	**TL**	**TL(z = 3.162; P = 0.002)**	**926.17**	**-**
logit($A_{success}$) = 0.03*TL - 0.25*Sex - 2.34*SW - 7.84	**TL, SW**	**TL(z = 6.004; P < 0.001); SW (z = -10.228; P < 0.001)**	**926.52**	**0.35**
logit($A_{success}$) = 0.03*TL - 2.37*SW - 7.03	**TL, SW**	**TL(z = 5.877; P < 0.001); SW (z = -10.382; P < 0.001)**	**926.63**	**0.46**
logit($A_{success}$) = 0.56 - 2.78*SW	SW	SW (z = -12.658; P < 0.001)	961.10	34.93

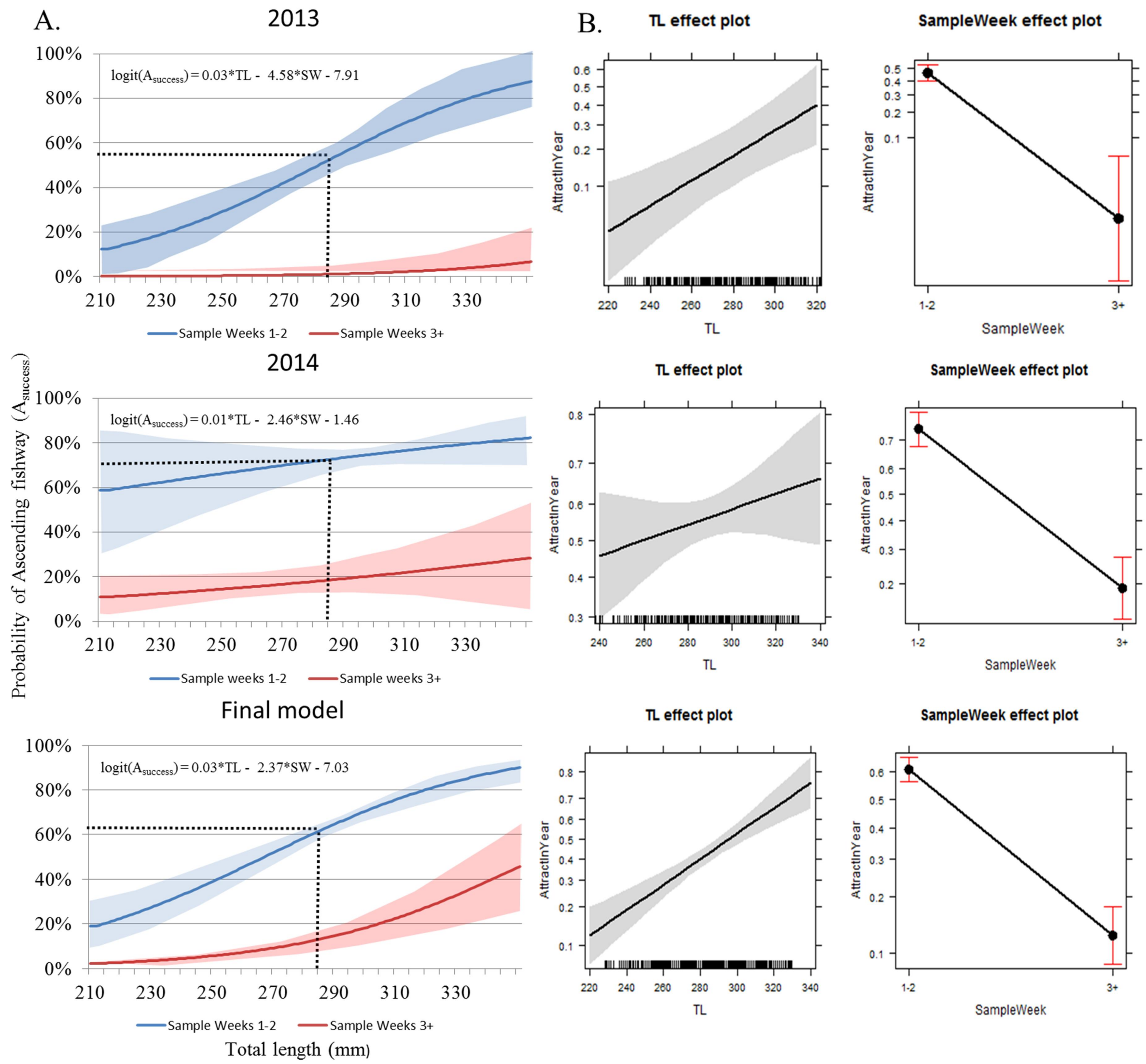

FIGURE 1.6.—Probabilities from binary logistic regression analysis (A.) with 95% confidence intervals and effect plots (B.) for attraction ($A_{success}$) in 2013, 2014, and a final model using both years of data. Dashed line indicates $A_{success}$ at mean length of Alewives returning to the fishway (285 mm TL).

TABLE 1.5.—Results of Welch's t-tests.

Comparison	Group 1 mean (± SD)	Group 2 mean (± SD)	*t*	*P*	df
Attraction total length (mm):	Not Attracted	Attracted			
2013	272 (± 19.1)	284 (± 18.7)	5.84	< 0.001	247.7
2014	281 (± 20.6)	295 (± 16.5)	8.73	< 0.001	406.5
Both	276 (± 20.2)	292 (± 18.0)	12.41	< 0.001	868.8
Ascended total length (mm):	Did not ascend	Ascended to top			
2013	274 (± 15.5)	289 (± 18.2)	-4.89	< 0.001	101.4
2014	291 (± 17.6)	299 (± 15.2)	-4.91	< 0.001	265.9
2015	298 (± 17.5)	312 (± 14.6)	-6.27	< 0.001	180.1
All years	291 (± 18.8)	300 (± 16.9)	-7.24	< 0.001	550.6
Attempts by sex:	Female	Male			
2013	3.3 (± 3.4)	3.3 (± 2.4)	0.02	0.98	105.4
2014	3.3 (± 2.5)	3.4 (± 2.5)	-0.8	0.42	464.3
2015	4.3 (± 4.4)	3.8 (± 3.7)	0.78	0.44	181.9
All years	3.5 (± 3.3)	3.5 (± 2.8)	0.08	0.94	732.7
Attempts by ascending:	Did not ascend	Ascended to top			
2013	2.5 (± 1.6)	3.7 (± 3.4)	-2.52	0.01	119
2014	3.3 (± 2.3)	3.4 (± 2.6)	-0.23	0.82	218.8
2015	4.1 (± 4.9)	4.1 (± 3.7)	0.05	0.96	56
All years	3.3 (± 3)	3.6 (± 3)	-1.13	0.26	354.9
Transit Time (hours) by Sex:	Female	Male			
2013	13.5 (± 17)	10.4 (± 10.7)	1.07	0.29	83.9
2014	10.6 (± 17.9)	10 (± 13.4)	0.38	0.70	317.3
2015	25.5 (± 34.8)	27.2 (± 34.1)	-0.33	0.74	161.6
All years	14.8 (± 24)	14.1 (± 21.4)	0.39	0.70	621.2
Movements by night/day:	Night	Day			
2013	15 (± 11.6)	257 (± 196.7)	-4.44	< 0.001	12.1
2014	31 (± 33.4)	360 (± 424.9)	-4.08	< 0.001	27.5
2015	17 (± 10.8)	227 (± 331.3)	-2.76	0.01	18.1
All years	23 (± 24.8)	296 (± 357.4)	-5.89	< 0.001	59.8

TABLE 1.6.—Logistic regression analysis results for probability of ascending the fishway ($R_{success}$). Best models (ΔAIC $\leq$ 2) are shown in bold. TL = total length, SW = sample week, YO = years since tagging.

Logistic regression model	Significant variables	Significance	AIC	ΔAIC
		2013		
logit($R_{success}$) = 0.06*TL -15.13	**TL**	**TL(z = 4.467; P < 0.001)**	**152.56**	**-**
logit($R_{success}$) = 0.05*TL - 0.10*Sex - 14.76	**TL**	**TL(z = 4.062; P < 0.001)**	**154.51**	**1.95**
logit($R_{success}$) = 0.05*TL - 4.81*Sex + 0.02*TL:Sex - 12.35	TL	TL(z = 2.481; P = 0.013)	156.12	3.56
logit($R_{success}$) = 0.93 - 0.87*Sex	Sex	Sex(z = -2.333; P = 0.020)	172.51	19.95
		2014		
logit($R_{success}$) = 0.03*TL + 0.34*Sex + 0.86*YO - 9.21	**TL, YO**	**TL (z = 4.551; P < 0.001)** **YO (z = 3.502; P < 0.001)**	**540.11**	**-**
logit($R_{success}$) = 0.03*TL + 0.87*YO - 7.98	**TL, YO**	**TL (z = 4.336; P < 0.001)** **YO (z = 3.550; P < 0.001)**	**540.29**	**0.18**
logit($R_{success}$) = 0.03*TL + 1.90*Sex + 1.02*SW + 10.34* YO - 0.01*TL:Sex - 0.01*TL:SW + 13.25*Sex:SW - 0.03*TL:YO - 17.94*Sex:YO - 8.88	TL	TL (z = 2.090; P = 0.037)	545.92	5.81
logit($R_{success}$) = 0.03*TL - 7.55	TL	TL (z = 4.318; P < 0.001)	551.97	11.86
		2015		
logit($R_{success}$) = 0.01*TL - 2.25			**221.76**	**-**
logit($R_{success}$) = 0.34*YO + 1.09			**222.31**	**0.55**
logit($R_{success}$) = 0.01*TL + 0.25*YO - 1.85			**223.32**	**1.56**
logit($R_{success}$) = 0.01*TL + 0.07*Sex + 0.24*YO - 2.05			225.28	3.52
logit($R_{success}$) = 3.61 - 0.01*TL - 9.06*Sex - 10.06* YO + 0.03*TL:Sex - 0.03*TL:YO + 6.44*Sex:YO			230.73	8.97
		Final		
logit($R_{success}$) = 0.01*TL - 3.19	**TL**	**TL (z = 2.119; P = 0.034)**	**457.55**	**-**
logit($R_{success}$) = 0.01*TL + 0.001*YO - 3.19	**TL**	**TL (z = 2.060; P = 0.039)**	**459.55**	**2.00**
logit($R_{success}$) = 0.01*TL - 3.06*YO + 0.01*TL:YO - 2.85	TL	TL (z = 1.795; P = 0.073)	461.36	3.81
logit($R_{success}$) = 0.16*YO + 1.26			461.86	4.31

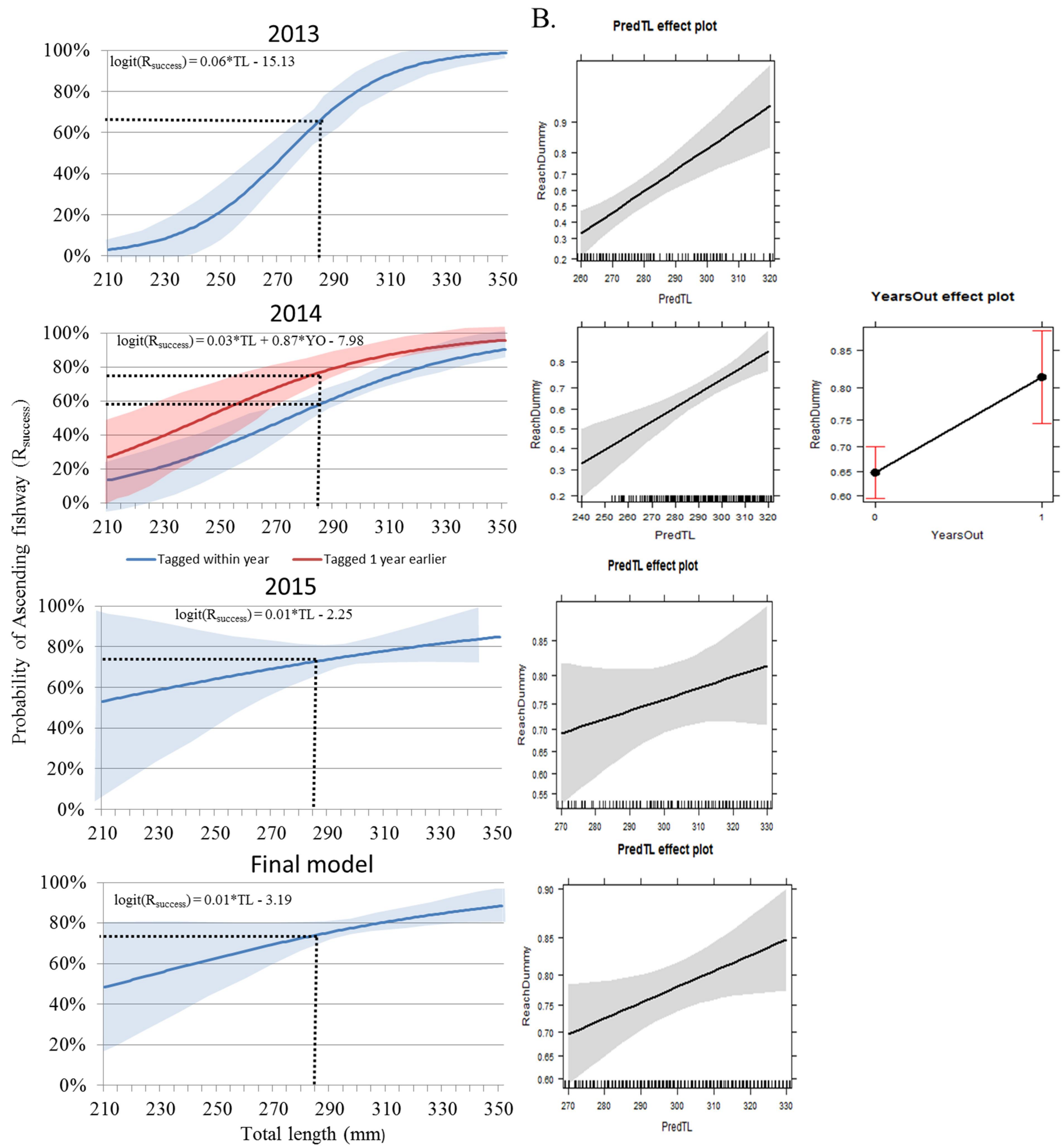

FIGURE 1.7.—Probabilities from binary logistic regression analysis (A.) with 95% confidence intervals and effect plots (B.) for ascending the fishway ($R_{success}$) 2013–2015 and a final model using all years of data. Dashed line indicates $R_{success}$ at mean length of Alewives returning to the fishway (285 mm TL).

TABLE 1.7.—Logistic regression analysis results for probability of passing the fishway ($P_{success}$). Best models (ΔAIC ≤ 2) are shown in bold. TL = total length and YO = years since tagging.

Logistic regression model	Significant variables	Significance	AIC	ΔAIC
	2013			
logit($P_{success}$) = 0.04*TL -12.40	**TL**	**TL(z = 3.722; P < 0.001)**	**155.96**	**-**
logit($P_{success}$) = 0.05*TL - 0.30*Sex - 13.64	**TL**	**TL(z = 3.613; P < 0.001)**	**157.49**	**1.53**
logit($P_{success}$) = 0.05*TL + 3.96*Sex + 0.01*TL:Sex - 15.54	TL	TL(z = -2.885; P = 0.004)	159.23	3.27
logit($P_{success}$) = -0.44*Sex - 0.41			170.28	14.32
	2014			
logit($P_{success}$) = 0.03*TL + 0.81*YO - 7.66	**TL, YO**	**TL (z = 4.200; P < 0.001) YO (z = 3.637; P < 0.001)**	**590.47**	**-**
logit($P_{success}$) = 0.03*TL + 0.35*Sex + 0.80*YO - 8.98	**TL, YO**	**TL (z = 4.457; P < 0.001) YO (z = 3.599; P < 0.001)**	**590.90**	**0.43**
logit($P_{success}$) = 0.03*TL + 0.87*Sex + 2.24* YO - 0.002*TL:Sex - 0.01*TL:YO - 6.68*Sex:YO - 9.03	TL	TL (z = 2.675; P = 0.007)	596.48	6.01
logit($P_{success}$) = 0.03*TL - 7.19	TL	TL (z = 4.170; P < 0.001)	602.43	11.96
	2015			
logit($P_{success}$) = 0.01*TL - 2.74			**264.25**	**-**
logit($P_{success}$) = 0.36*YO + 0.50			264.69	0.44
logit($P_{success}$) = 0.01*TL + 0.27*YO - 2.30			265.55	1.30
logit($P_{success}$) = 0.01*TL + 0.06*Sex + 0.28*YO - 2.10			267.51	3.26
	Final			
logit($P_{success}$) = 0.02*TL + 0.34*Sex - 4.75	**TL**	**TL (z = 2.663; P = 0.008)**	**542.65**	**-**
logit($P_{success}$) = 0.01*TL - 3.51	**TL**	**TL (z = 2.286; P = 0.022)**	**542.97**	**0.32**
logit($P_{success}$) = 0.02*TL + 0.34*Sex - 0.11*YO - 4.93	**TL**	**TL (z = 2.671; P = 0.008)**	**544.40**	**1.75**
logit($P_{success}$) = 0.13*Sex + 0.72			547.87	5.22
logit($P_{success}$) = 0.01*TL - 5.28*Sex - 3.67*YO + 0.02*TL:Sex + 0.01*TL:YO - 1.91			550.79	8.14

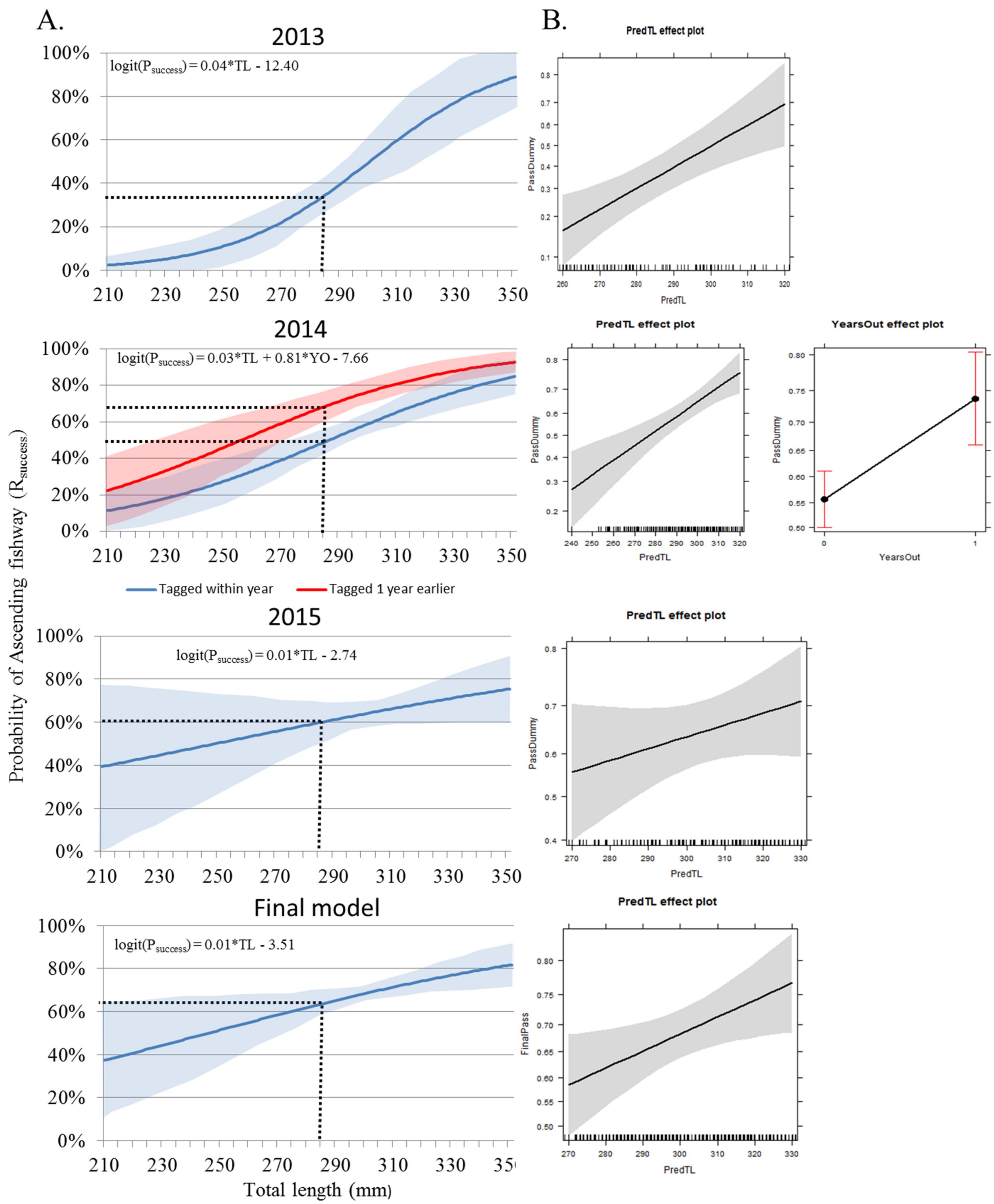

FIGURE 1.8.—Probabilities from binary logistic regression analysis (A.) with 95% confidence intervals and effect plots (B.) for passing the fishway ($P_{success}$) 2013–2015 and a final model using all years of data. Dashed line indicates $P_{success}$ at mean length of Alewives returning to the fishway (285 mm TL).

1.7; Figure 1.8). As a result of volitional descent after ascending to the trap, $P_{success}$ model results were nearly parallel to those of $R_{success}$ but were about 10% less at corresponding total lengths (Figures 1.7 and 1.8). Final model results for a 285 mm fish had an $R_{success}$ of 74% and a $P_{success}$ of 64% (Figures 1.6–1.7). Final probability of passage success for a fish at 285 mm is an $A_{success}$ of 61% and a $P_{success}$ of 64% for an overall probability of 39%.

Behavior and diel pattern of movements

Most fish only ascended to the top of the fishway once, but over the three years 51 fish ascended to the trap twice after volitionally descending the fishway. Five fish ascended to the trap on three separate occasions (Table 1.3). The time individual fish spent in the trap before descending the fishway was as short as 2s to as long as 97.6 hours. Nighttime movements were minimal in all three years, only accounting for ~5% each day and were significantly less than during the daylight hours (t = -5.89, P < 0.001; df = 60; Table 1.4). Movements began daily at sunrise, generally increasing until just before sunset, when a higher proportion of downward movements occurred before most overnight activity ceased (Figure 1.9).

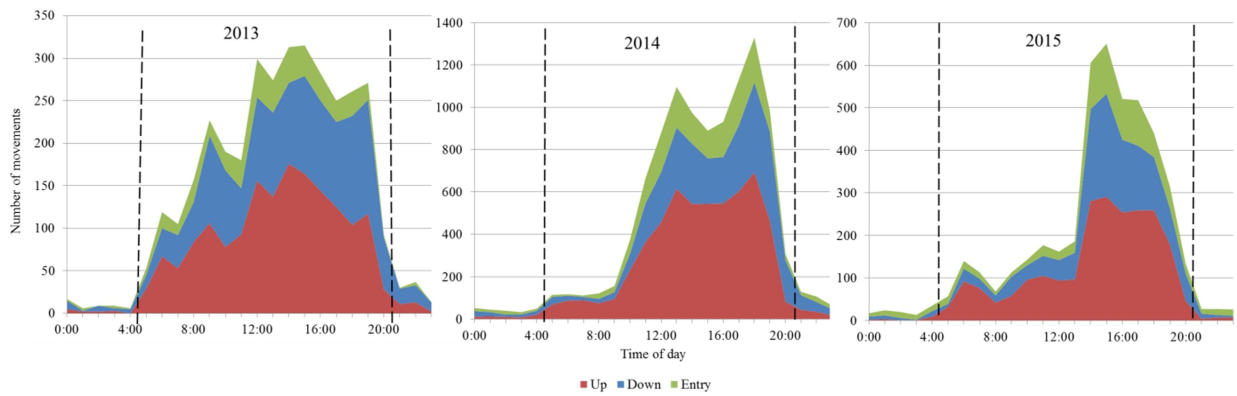

FIGURE 1.9.—Number of movements by time of day. Dashed lines indicate twilight times of sunrise and sunset.

Discussion

In the northeast, many fishways were constructed to benefit Atlantic salmon, but as those populations have declined or become extirpated from many coastal systems, the focus of these fishways has been for restoration efforts of river herring, both Alewife and Blueback Herring, in these same rivers. The demonstrated ability of river herring to quickly repopulate a system when provided access to essential freshwater spawning habitat makes the presence of fishways an important tool in the suite of restoration, monitoring, and management efforts (Pardue 1983; Lichter et al. 2006). However, even with the prolonged operation of fishways, many constructed decades ago, very little attention has been placed on measuring the efficiency of successful passage of river herring through the structures. This study used PIT tagging to gain insight into the attraction rates, passage efficiency, size and species selectivity, limitations in total passage due to saturation levels, and diel behavioral patterns of Alewife movements. Two years of tagging and data collection over three consecutive spawning seasons provides data for these objectives.

Well-designed fishways can allow efficient passage once entered, yet their effectiveness relies on successful attraction, which can be the most critical part of a fishway design (Williams et al. 2012). Bunt et al. (2012) conducted a comprehensive review of available data from 116 previous peer-reviewed scientific studies of fishway attraction and passage efficiency, covering 35 fishways, 26 species, six countries (Canada, Denmark, Russia, Scotland, Sweden, and the United States), and four fishway types (pool-and-weir, Denil, vertical-slot, and nature-like bypass channels). In that review, attraction efficiency of Denil fishway studies ranged from 21–100% with a mean of 61% and median of 57% (Bunt et al. 2012). Attraction rates found in this study were 33% in 2013 (lower than the published mean and median), 57% in 2014 (equal to the published median value), and 61% in the final logistic regression model (equal to the published mean), all within the published ranges.   Lower attraction in the first year compared to the second, may have been due, in part, to the exclusion of fish tagged earliest in the spawning run as a result of equipment error. Logistic regression effects analysis showed that fish were significantly more likely to enter the fishway if they were tagged in the first two weeks of the spawning season and if they were tagged at least one year earlier (Figure 1.6). It is believed that inclusion of fish tagged in the first week in 2013 would have resulted in an attraction value closer to that observed in 2014.

As fish were captured, tagged, and released within 100 m of the entrance to the fishway in this study, it was assumed that all were available for attraction to the fishway, but low attraction rates observed may have been related to behavioral changes, handling stress, or mortality as a result of the tagging process. Mortality related to tagging and tag expulsion are not believed to be significant factors in the low attraction rates, as previous tagging studies with Alewives exhibited very low mortality rates and high tag retention (Smith et al 2009; Franklin et al. 2012), but behavior of downward movement following tagging, referred to as “fallback”, has been reported in various alosines (Beasley and Hightower 2000; Hightower and Sparks 2003; Bailey et al. 2004; Olney et al. 2006; Frank et al. 2009).   If this behavioral response was exhibited by some of the tagged fish in this study, it would result in underestimates of attraction. Median times of 78.5 hours in 2013 and 95.7 hours in 2014 between the time of release and the first detection at the fishway does suggest that the capture and tagging process induced stress that required a recovery/acclimation period before fish resumed normal activity. Use of an additional antenna located further below the fishway entrance may have better estimated true attraction rates in this study, but was not possible due to environmental constraints. Franklin et al. (2012), the only other known fishway study with river herring, included antennas downstream of studied fishways in two river systems (Town Brook and East River). Attraction values in that study were as low as 29% at a pool-and-weir fishway, but were 100% for both Denil fishways measured (Franklin et al. 2012). Despite the high reported attraction rates, only 43% of tagged fish in Town Brook and 60% of tagged fish in East River were detected by the antenna array in the previous study (Franklin et al. 2012). These results of all tagged fish are much closer to the attraction values of the present study which assumed all tagged fish were available for attraction to the fishway. This is likely a better comparison between the previously reported results and the attraction rates in this study, considering the absence of a downstream antenna. The percentage of tagged fish entering the fishway and able to ascend to the trap was very similar in the last two years of the study, 77% and 78%, but the rate in 2013 was lower (64%). The lower values from 2013 might again be explained in part by the exclusion of the fish tagged in the first week of the spawning run that year. In both years that fish were tagged, the proportion of fish detected and recorded to have ascended to the top of the fishway was highest for the fish tagged during the first two tagging dates within each year. Furthermore, in 2014 fish that were tagged 1 year prior to the monitoring season, had significantly greater success (84%; $z = 3.550$; $P < 0.001$) in ascending to the top of the fishway than those tagged within that year (72%), and all fish in 2015, tagged either one or two years prior, had a higher success rate than fish tagged within season for both 2013 and 2014. These higher levels provide evidence in support of a reduced passage efficiency likely related to tagging stress. Therefore, the average value of successful passage of fish entering the fishway for 2014 and 2015, 67%, may be the best estimate. This is similar to $R_{success}$ (74%) from the final logistic regression model of successful ascent, which only uses fish tagged at least one year prior to remove the tagging effect. As was found for attraction efficiency, passage efficiency results of the present study (61%) are within the range and similar to the mean and median values reported for other studies of Denil fishways (range=0–97%, mean=51%, median=38%), but are generally low in comparison to a previously published study of Alewives which ranged between 21% and 97%, with a mean value of 74% (Bunt et al. 2012; Franklin et al. 2012). However, the technical fishways examined by Franklin et al. 2012 were much smaller (length=3–14 m, elevation=0.29–0.91 m) than that in the current study (length= 53 m, elevation=6.9 m) and some fishways were only accessible to individuals who had already successfully ascended fishways downstream, which could bias results by including a higher percentage of fish more capable of ascending fishways.

The incorporation of a trap area in the design of a fishway is valuable in assisting with collection of Alewives for biological sampling and for retaining thousands of fish for trap-and-transport stocking activities, but may also negatively affect potential fish passage. There is only a short distance, with no elevation change between the top of the fishway and the exit at the counting tube, but Alewives school in the hundreds or thousands once in the trap rather than continuing in a straight line through the counting tube. The time an individual fish spent in the trap varied widely, with residence times as short as 2 seconds and as long as 4 days, with median times between 2.9 and 15.9 hours, after which some fish passed into the river above through a counting tube or were physically passed with a net, whereas others volitionally left the trap and descended down the fishway. Leaving the trap to descend the fishway instead of passing upriver was most apparent in 2013, when 33 of the 79 Alewives that ascended to the trap left by descending the fishway and never ultimately passed above. Similarly, but at a much smaller proportion, not all fish ascending to the top of the fishway in 2014 and 2015 were successful in passing because they descended the fishway rather than utilizing the counting tube. This study shows that annual passage numbers through the fishway are reduced by as much as 42%, as was seen in 2013, when fish descend the ladder after some time spent in the trap after a successful ascension. Logistic regression analyses and the measured percentages of fish ascending to the top compared to those that passed show that trap likely reduces passage efficiency by 10% on average. Increased efficiency may be achieved by eliminating access to the larger trap area for fish ascending to the top of the fishway during times when collection for sampling and stocking are not necessary. Also, automated counting methods that are able to take advantage of a larger exit area from the trap into the river above, such as multiple counting tubes or video monitoring could provide gains in passage numbers.

Passage inefficiencies observed in this study seemed to be related to diel movement patterns of Alewives and possible fishway saturation limits. The effect of time of day on fishway passage success has been found in other studied species, including salmonids (*Oncorhynchus nerka*; Naughton et al. 2005) and various other freshwater (Thiem et al. 2013) and anadromous species (Keefer et al. 2013). Caudill et al. (2007) found that Chinook Salmon (*Oncorhynchus tshawytscha*) were between one-fifth to less than one-twentieth as likely to pass during nighttime hours, and was the strongest and most significant effect on passage. Thiem et al. (2013) found variation by species with Freshwater Drum (*Aplodinotus grunniens*) and Channel Catfish (*Ictalurus punctatus*) moving primarily at night, Sauger (*Sander canadensis*) and Walleye (*Sander vitreus*) making crepuscular movements, and many other species moving exclusively during daylight hours. A diel pattern of movement by tagged Alewives was evident and consistent throughout all three of the monitored years. Figures 1.6 and A.1–A.3 show a pattern of upward movements beginning with the first hours of sunlight on most days and continuing throughout most of the day. A steep and sudden decline in upward movements occurred at sunset on most days and few upward movements of tagged Alewives (~5% or less) occurred during times of darkness. This is consistent with previous findings of studied Alewives in Massachusetts, where 89% and 72% of Alewives in Town Brook and East River, respectively, began their first attempt during daylight hours (Franklin et al. 2012). Furthermore, the onset of darkness triggered descent of the fishway to some extent or exiting the fishway by some fish, leading to reduced overall passage. Contrary to findings of this study, passage of river herring in other states has been observed occurring at night and in some systems occurs primarily at night (B. Gahagan, Massachusetts Division of Marine Fisheries, personal communication; D. Ellis, Connecticut Department of Energy and Environmental Protection, personal communication). It is difficult to explain why only 5% or less of all movements occurred during the nighttime hours and why nearly two thirds of those movements in all three years were downward (Figure 1.6). Possibly, water turbulence created by the fishway baffles and the confinement of the 1 m wide fishway may instinctually cause Alewives to cease movement activities for their safety during hours of darkness. Causes remain unknown, but the relative absence of movement within the fishway during nighttime hours observed in this study suggest that further investigation into the causes of this effect should be completed to determine if there is a relationship to fishway design.

A second, but less pronounced pattern of increasing upward movements from sunrise to mid-day hours, followed by a period of limited movements, and then a second increase in upward movement until sunset was observed (Figures A.1–A.3). Overlaying the time that fish were physically removed from the trap, showed that the second peak of activity generally increased rapidly and began immediately following the event. This pattern suggests that the fishway may quickly become saturated during the peak periods of the spawning run, further reducing the passage efficiency of the fishway. Saturation may also help to explain the limited upward movements during nighttime hours discussed previously. During the days of high abundance of Alewives, fish refilled the trap as quickly as it could be emptied. Strong evidence for fishway saturation limiting nighttime passage can be seen between May 3 and May 7, 2014 (Figure A.2). On each day during that period, there was very little upward movement of tagged fish during a period from the night before extending through as late as 3:00 PM the following day. On each of those days there was a large increase in upward movements following cleanout of the trap, but it declined before dark and nearly ceased by sunset. The pattern suggests that although the fishway trap was emptied mid-day, it attained capacity before dark, and remained at a saturation level until it was emptied the next day. It is important to note that although the fishway is only emptied by biologists once per day, fish are capable of exiting the fishway at all times through the counting tube. Reduced passage in relation to fishway saturation does not seem to be consistent across species. Passage rates of Chinook Salmon in the Columbia River increased with higher numbers of Chinook in the fishway at the same time, but in the same study passage rates were reduced with increases in density of American Shad (*Alosa sapidissima*) in the fishway (Caudill et al. 2007).

This study shows a reduction in motivation of gravid Alewives to continue attempts to ascend the fishway after the first few weeks of the spawning season. This study captured and tagged fish throughout the spawning run for each of the first two seasons of monitoring. The proportion of fish attracted to the fishway, ascending to the trap, and successfully passing was highest in the fish tagged earliest in each season. A steep and rapid decline in the proportions of fish entering and ascending the fishway was observed for fish tagged more than ten days into the spawning run each year. None of the Alewives tagged on the latest dates in both 2013 and 2014 were recorded as entering the fishway during the year in which they were tagged. Logistic regression results showed that fish sampled in the first two weeks of the spawning run had a significantly higher likelihood of entering the fishway than those tagged after the second week. Tagging procedures were the same on all tagging dates and there were no observed signs of increased stress or mortality on the tagging dates later in the season. These findings of diminished passage as the spawning season progresses are contrary to those found in studies of salmonid species, where it was concluded that individuals migrating late within runs tended to migrate faster through fishways (Quinn and Adams 1996; McLean et al. 2004; Caudill et al. 2007).

Migration barriers can act as a selective force on fish size and can ultimately shift life history traits (Sigourney et al. 2015). Fishways, such as the one used in this study, may be altering population demographics through selectivity associated with their designs. Identifying the fishway selectivity on the size and species of river herring able to successfully ascend is important since much of the information used by management agencies is collected at the top of a fishway or in the freshwater sections of rivers above a fishway. Population demographics (e.g. length, sex, and species distributions) produced only from river herring collected at the top of or above a fishway may be biased as a result of this selectivity. This study found a selectivity for larger fish, as Alewives that were able to successfully ascend the fishway had a significantly greater total length in all years than those that attempted to ascend the fishway, but were unsuccessful. Similarly, although they were not included in the analysis, the 49 Blueback Herring tagged exhibited minimal attraction to the fishway and no successful passage. The limited use of this fishway by Blueback Herring is evidence of selectivity against the species as a likely result of the fishway's selectivity towards larger fish, as Blueback Herring are smaller in overall body size and total length than Alewives of the same age and may not attain equivalent maximum sizes (Fay et al. 1983; Loesch 1987; Collette and Klein-MacPhee 2002). In contrast consistent, negative relationships between body length and fishway passage success have been reported for Pacific (Caudill et al. 2007) and Atlantic salmon species (Laine et al. 2002; Sigourney et al. 2015) as well as Brown Trout (*Salmo trutta*; Haugen et al. 2008). Size selection can have both immediate and long-term consequences for population dynamics such as smaller size and age at maturity (Sigourney et al. 2015). Although conventional wisdom is that significant evolutionary change will only rarely be observed at ecological time scales, Haugen et al. (2008) points out that several recent studies have reported rapid evolution in fish populations (within a few generations) within the last few decades. A better characterization of river herring populations in systems where fishways provide sole access should incorporate sampling of the population in the areas below the first fishway. In the Lamprey River, as well as some other coastal rivers where fishways are operated in New Hampshire, Blueback Herring are rarely observed during sampling at the top of the fishway, but are the primary species captured when sampling occurs in the tidal waters immediately below the fishway (M. Dionne, New Hampshire Fish and Game Department, unpublished data.).

CHAPTER 2

RADIO TELEMETRY OF ALEWIFE (*ALOSA PSEUDOHARENGUS*) TO ASSESS WADLEIGH FALLS AS A BARRIER TO MIGRATION IN THE LAMPREY RIVER, NEWMARKET, NEW HAMPSHIRE

Introduction

New Hampshire's coastal rivers once supported abundant runs of Alewife (*Alosa pseudoharengus)* and blueback herring (*A. aestivalis)*, collectively referred to as river herring (Jackson 1944). As an anadromous fish, river herring spend most of their lives in marine waters and undertake vernal spawning migrations often to the same rivers from which they hatched (Collette and Klein-MacPhee 2002). In freshwater, juvenile river herring serve as prey for a number of fish species, including Yellow Perch (*Perca flavescens*), White Perch (*Morone americana*), Largemouth Bass (*Micropterus salmoides*), Smallmouth Bass (*Micropterus dolomieu*), pickerel (*Esox* spp.), trout and other salmonids, as well as birds, turtles, and mammals. In marine waters, they are an important food source for Striped Bass (*Morone saxatilis*), Bluefish (*Pomatomus saltatrix*), tunas (*Thunnus* spp.), Atlantic Cod (*Gadus morhua*), and Haddock (*Melanogrammus aeglefinus*). Currently, the primary use of commercially and recreationally harvested river herring is to provide bait for the commercial lobster fishery and recreational saltwater anglers targeting Bluefish and Striped Bass. Unfortunately, river herring populations have exhibited drastic declines throughout much of their range (Limburg and Waldman 2009; ASMFC 2012) and were listed as a "species of concern" by the National Oceanic and Atmospheric Administration's Fisheries Service in 2006. While the exact cause(s) of this population decline are unknown, the most likely threats include: loss of habitat due to decreased access to spawning areas from the construction of dams and other impediments to migration, habitat degradation, fishing pressure, and increased predation due to recovering Striped Bass populations (ASMFC 2012).

River herring and other diadromous species have been denied access to historical, freshwater spawning habitat since dam construction during the nineteenth century textile boom along the Atlantic Coast, including most New Hampshire coastal rivers. Methods to restore river herring runs in other areas have been through stocking of Alewives (Rounsefell and Stringer 1945; Collette and Klein-MacPhee 2002), construction of fishways, or removal of defunct dams (Havey 1961).

The Lamprey River is a tributary to Great Bay Estuary in coastal New Hampshire. The river runs approximately 80 km from the headwaters in Northwood, New Hampshire and empties into Great Bay in Newmarket, New Hampshire (Figure 2.1). Although many dams exist, both active and remnant, along the length of the Lamprey River and its tributaries, four with various levels of fish passage are currently known to be primary impediments to river herring on the main stem (Figure 2.1). Restoration of river herring populations in the Lamprey River began with construction of a Denil fishway in 1972 at the Macallen Dam, an 8.2 m high low-head dam with a spillway width of 45.7 m located at the head-of-tide (rkm 3.0) in Newmarket, New Hampshire. This fishway allowed anadromous fish, including river herring, to access approximately 5.6 km of potential spawning habitat above the head-of-tide before the next barrier, which is the Wiswall Dam (rkm 8.6). It has a height of 5.5 m and a width of 61.0 m. As a result, for the past 18 years, the New Hampshire Fish and Game Department has transferred river herring by stocking truck from the head-of-tide Macallen Dam in Newmarket, New

Hampshire, to areas further upstream of the multiple man-made barriers; specifically the Wiswall, breached Wadleigh Falls, Bunker Pond, and Pawtuckaway Lake dams. In 2011, the Bunker Pond Dam (rkm 41.5) in Epping, New Hampshire, was removed. Removal of Bunker Pond Dam occurred simultaneously with the construction of a fishway 33 km downriver at the Wiswall Dam. The new Wiswall fishway and removal of Bunker Pond Dam created the potential to allow river herring access to more than 70 km of spawning habitat. However, the breached Wadleigh Falls Dam, located between the two locations at rkm 21.4 with a height of 4.0 m, a width of 91.4 m, and no constructed fish passage, has never been objectively examined for its efficacy in river herring passage (Figure 2.2).

With the opening and operation of the Wiswall Dam fishway for the first time in the spring of 2012, biologists observed several thousand river herring at the base of the Wadleigh Falls Dam, which for the first time in more than a century arrived there on their own. River herring were seen making several attempts at negotiating the high flows and steep drop-offs that the breached dam created. Unfortunately, no river herring were observed successfully passing the man-made barrier. In an effort to better understand the movements of river herring upon arriving at the breached Wadleigh Falls Dam location in Lee, New Hampshire and their ability (or inability) to pass over the structure, a radio tagging study was conducted during the spawning migration in the spring of 2013.

The primary objective of this study was to determine if the breached dam is an impassable barrier for river herring and therefore represents the upper most extent of their annual spawning run in the Lamprey River. Secondary objectives of the study were to examine channel selection of tagged fish when encountering the split in the river below Wadleigh Falls, observe the movement and possible searching patterns of river herring once encountering a challenging barrier along their migratory route, and to measure the amount of time river herring spend within the river system from entry and exit at the head-of-tide.

Methods

Passive integrated transponder (PIT) tagging

Fish were PIT tagged following the methods outlined in Chapter 1 on seven dates between April 26 and May 31, 2013 during the spawning migration. Methods of capture and tagging were consistent on all days. Only fish tagged on April 30, 2013 were used in the analysis, as only fish tagged on that date was recorded at the Wiswall Dam fishway (Table 2.1).

The array of eight loop antennas outlined in Chapter 1 was used at Macallen Dam fishway, and a smaller array of two loop antennas constructed in the same way were placed in the Wiswall Dam fishway. One antenna was installed at the entrance to the fishway and a second on the last baffle before the exit of the fishway. The Wiswall fishway does not have a trap area and fish were able to freely swim through the ladder into the impounded river above. Detections from these antennas were continuously recorded using an Oregon RFID multiplexer with a tuning box for each antenna. The multiplexer was placed in a weather-tight container on the lower section of the Wiswall fishway and was powered by two deep-cycle marine batteries. The lifespan of the batteries varied based on the activity of detections at each receiver, but generally lasted for four days between battery changes. Data were downloaded during battery changes and a marker tag was left attached to the baffle where the uppermost antenna was mounted for the duration of the study. Signals from this tag were recorded every 30 minutes to ensure that the multiplexer was working properly.

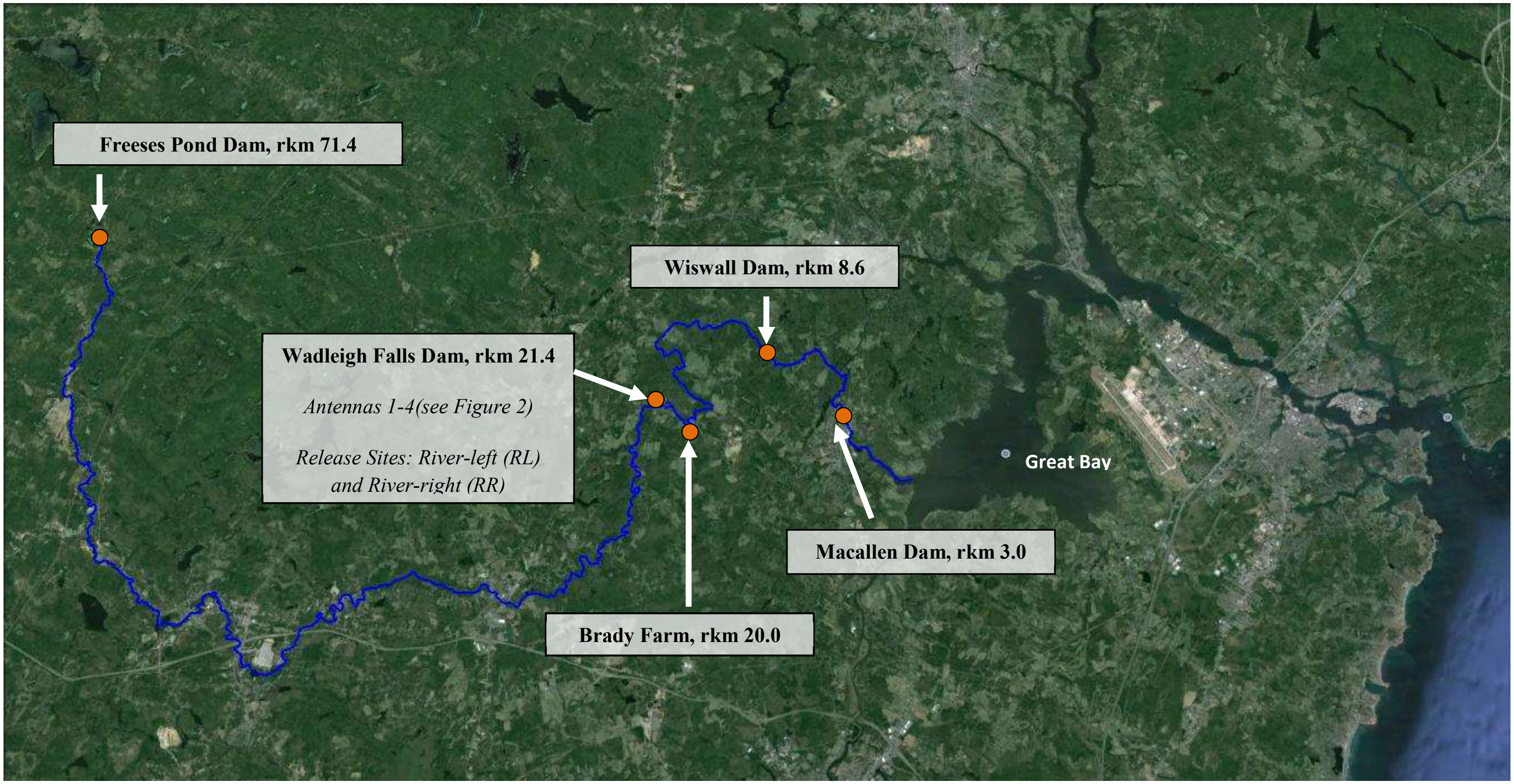

FIGURE 2.1.—Dams, release sites, and stationary telemetry receiver locations for a telemetry study of Alewives during the 2013 spawning migration in the Lamprey River, New Hampshire.

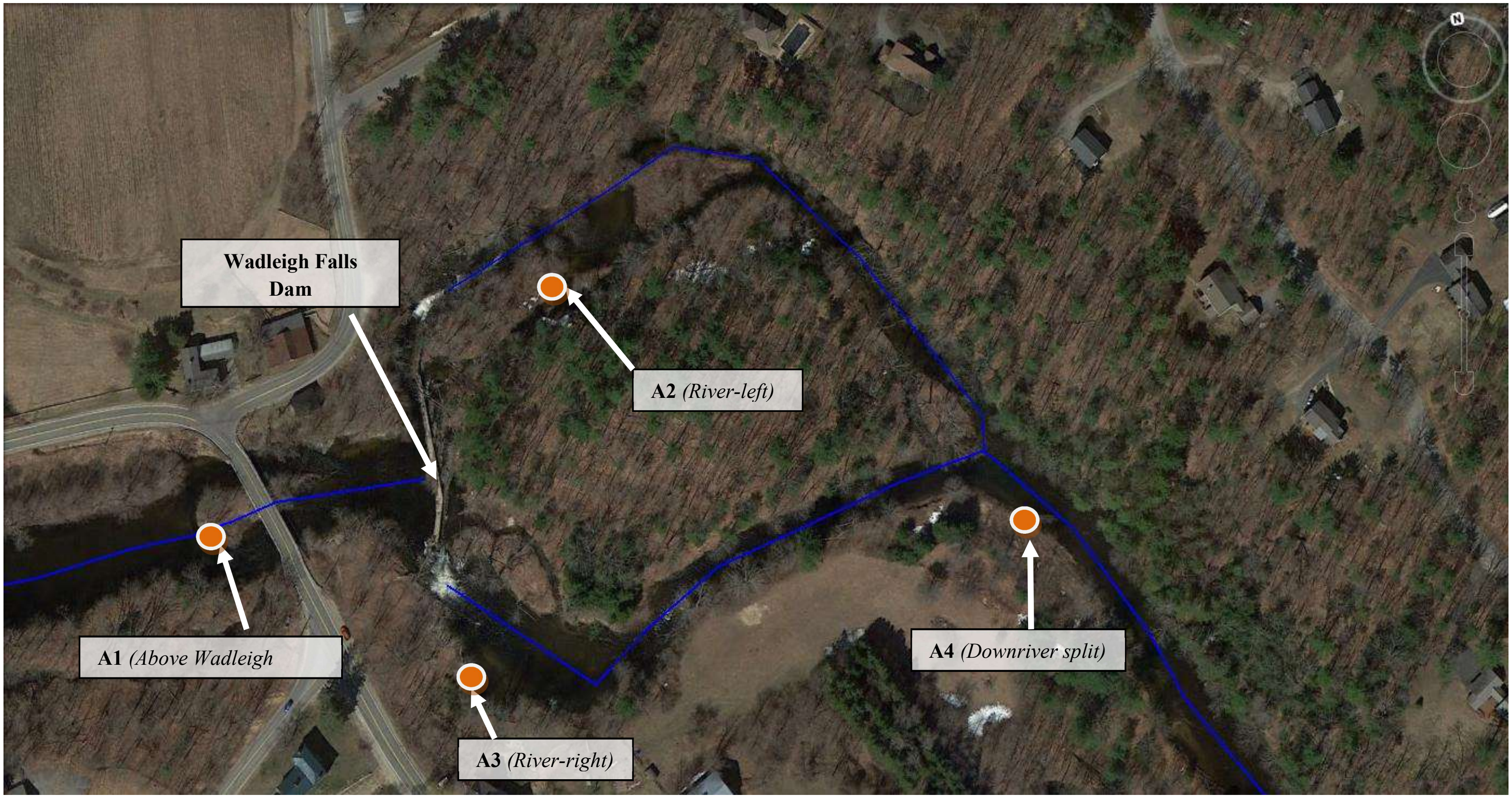

FIGURE 2.2.—Stationary telemetry receiver locations at the breached Wadleigh Falls Dam location on the Lamprey River, New Hampshire.

TABLE 2.1.—Number (%) of Alewives tagged and detected at the Macallen Dam and Wiswall Dam fishways, as well as the transit times between determined using PIT tags during the 2013 spawning migration in the Lamprey River, New Hampshire.

		Macallen fishway		Wiswall fishway	Transit time (d)			
Tagging date	Number tagged	Number entered	Number passed	Reached	Mean	Min	Max	Mean speed (rkm/hr)
April 26	251	*(Excluded from analysis due to software conflicts)*						
April 30	200	123 (62%)	46 (37%)	24 (52%)	4.8	1.2	24.1	0.05
May 7	17	5 (29%)	0 (0%)	0 (0%)	-	-	-	-
May 8	33	2 (6%)	0 (0%)	0 (0%)	-	-	-	-
May 13	50	1 (2%)	0 (0%)	0 (0%)	-	-	-	-
May 17	21	0 (0%)	0 (0%)	0 (0%)	-	-	-	-
May 31	49	0 (0%)	0 (0%)	0 (0%)	-	-	-	-

During data processing of PIT records, a river herring was classified as having passed Macallen Dam fishway if it was successfully recorded passing antennas in consecutive order with the last detection at the uppermost antenna in the array. An individual fish was only classified as arriving at the Wiswall Dam if it was detected at either the upper or lower antenna in the ladder. The transit time from Macallen Dam to Wiswall Dam for those fish detected was the difference in minutes from the time of passage at Macallen Dam to the first detection at either antenna in the Wiswall Dam fishway.

Radio Tagging

Adult river herring were captured at the Wiswall Dam fishway in Durham, New Hampshire as they migrated upstream. This sampling location was chosen over the head-of-tide dam because the condition of sampled fish which had entered the river from tidal waters and successfully migrated the 5.6 km upriver to the Wiswall Dam would better represent the physiological condition of individual fish if they had migrated to the breached Wadleigh Falls

Dam location on their own. Additionally, collecting fish at this location rather than at the Macallen Dam at the head-of-tide reduced transfer time to release sites to only 10 minutes and river distance by approximately 32%.

Fish were removed from the lowermost section of the Wiswall Dam fishway by lowering a 1.22 m diameter x 0.635 cm mesh cast net into the ladder from above. Once collected, fish were placed in plastic containers containing 113.5 L of water, removed from the same section of the fishway. Fish that appeared healthy based on active swimming, minimal scale loss, and no apparent forceful gilling were tagged, while those that appeared in impaired health or greater levels of handling stress were returned to the river without tagging. Lotek NTQ-4-2S uniquely coded transmitters (7.6 X 15.1 mm; 23.5 cm antenna; 1.4 g air weight) with a 163 d operational lifespan were used. The tags operated at two frequencies, 150.370 MHz and 150.450 MHz, and had evenly distributed burst rates of the tags between 4.7, 4.8, 4.9, 5.0, and 5.1 seconds to avoid signal collision. During tagging, fish were removed from the holding container to measure and record its total length (±1 mm), sex, and species. The fish were then held under water in the container and a tag was inserted esophageally into its stomach using a 196 mm x 6 mm diameter drinking straw as the fish remained submerged. The tagging process of each fish typically took less than 30 s. Once tagged, fish were placed into a 700 L recovery tank containing 530 L of river water with aeration and observed for 10 minutes before transported to a release site. If a fish was observed not actively swimming or exhibited physical signs of excessive stress, it was removed from the tank, the tag removed to be used later, and the fish returned to the river before transport. This occurred on two occasions. Fish were tagged on two dates in 2013 and capture and tagging methods were consistent on both days.

Releases of tagged fish occurred at three locations between the tagging area and the breached Wadleigh Falls Dam study area (Figures 2.1 and 2.2). All release sites were upriver from tagging location and required transport. Nearly half (48%; $N = 45$) of tagged fish were released at Brady Farm (BF), a location 11.1 km upriver and 1.4 km below the breached Wadleigh Falls Dam (Table 2.2). This release site was chosen to examine channel selection by tagged fish, as it was approximately 1.1 km downstream of the location where the river split into two isolated channels that each continue to the Wadleigh Falls Dam about 0.4 km further upstream (Figures 2.1 and 2.2). The remaining tagged fish were released immediately below the breached Wadleigh Falls Dam 12.5 km upriver, split evenly between each side of the island on river-left (RL; $N = 24$) and river-right (RR; $N = 24$; Table 2.2). Previous alosine telemetry studies have shown that various proportions of tagged fish may immediately head downriver after being released in response to the stress from the tagging and transport process (Dodson et al. 1972; Bell and Kynard 1985; Barry and Kynard 1986; Chappelear and Cooke 1994; Beasley and Hightower 2000; Moser et al. 2000; Hightower and Sparks 2003; Acolas et al. 2004; Bailey et al. 2004; Sprankle 2005; Olney et al. 2006; Frank et al. 2009). Therefore, releases immediately below Wadleigh Falls were made to ensure that some tagged fish would be present at the area of primary interest in this study.

Antennas

Six stationary radio telemetry receivers (four LOTEK SRX-DL3 and two LOTEK SRX-400) with three-element yagi directional antennas (Sigma Eight) were deployed at locations along the study area of the river (Figures 2.1 and 2.2). The gain of all receivers was set to 50, with the exception of the receiver located at the Wiswall Dam. This receiver was set to 75, the greatest detection range possible before signal noise became excessive. The scan time of all receivers was set for 6.0 s on each frequency which covered the range of burst intervals (4.7–5.1 s) for tags on each frequency. Receivers recorded tag detections continuously with only minor interruptions in coverage on some receivers due to low battery power or attaining a receiver's memory capacity. Each detection record included the date, time, channel, unique tag number, and power of the detection. Range tests for receivers were conducted before and after the sampling period and data download frequency varied based on the quantity of tag detections recorded to avoid excessive memory use of the receivers.

Detection Records

Detection records with a value of "255" were classified as signal collision and values of "999" were classified as noise. All detections during the first 15 minutes post-release were excluded and unique tag numbers that were detected on multiple receivers at the same time were considered to be overlap detections. The actual location of a tagged fish was selected by the most consecutive detections within a five minute period at either of the antennas and by the greatest signal strength. If a period greater than five minutes occurred between consecutive detections at a receiver location, the fish was classified as absent from the site. Five minutes was selected because the time that fish were recorded moving between antennas surrounding Wadleigh Falls (A1, A2, A3, A4) was less than five minutes more than 75% of the time (Figure 2.3). A movement was classified as "fallback" if it was released at site RL or RR and was detected downstream at the Wiswall Dam within 48 hours, or if released at site BF and never detected at any of the antennas upriver (A1, A2, A3, A4). The timeframe of 48 hours was used following data review because 75% of all fish moved between Wadleigh Falls and Wiswall Dam within 48 hours.

TABLE 2.2.—Total lengths and sex distributions of radio tagged Alewives for a telemetry study at the breached Wadleigh Falls Dam location during the 2013 spawning migration on the Lamprey River, New Hampshire.

	N			Total length (mm)								
				Mean			Min			Max		
Release site	Male	Female	All	Male	Female	All	Male	Female	All	Male	Female	All
River-left (RL)	10 (42%)	14 (58%)	24	292.6	298.7	296.2	268	272	268	317	316	317
River-right (RR)	16 (67%)	8 (33%)	24	283.5	281.5	282.8	250	268	250	310	303	310
Brady Farm (BF)	21 (47%)	24 (53%)	45	289.6	298.6	294.4	263	262	262	317	325	325
All release sites	47 (51%)	46 (49%)	93	288.1	295.7	295.7	250	262	250	317	325	325
Samples from fishway	146 (49%)	154 (51%)	300	287	300.6	293.9	242	260	242	318	338	338

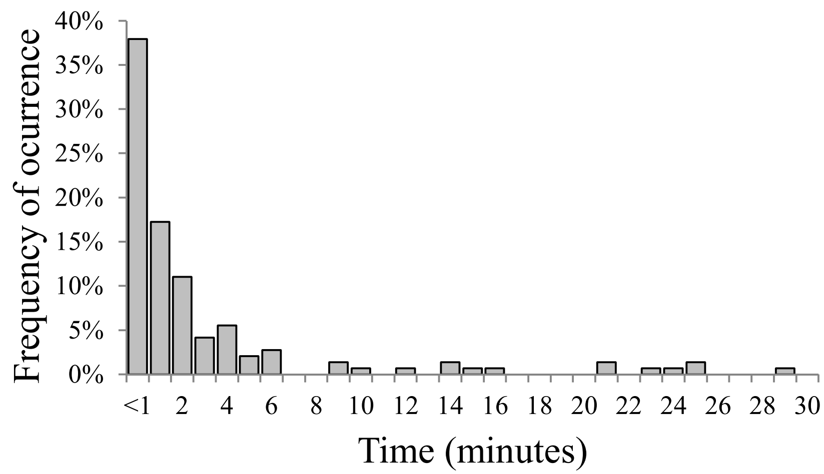

FIGURE 2.3.—Frequency of duration between detections at adjacent receivers located near Wadleigh Falls (A1, A2, A3, A4). Seventy eight percent of the durations were five minutes or less.

Results

Passive integrated transponder (PIT) tagging

A total of 621 Alewives were PIT tagged below the Macallen Dam on seven dates between April 26, 2013 and May 31, 2013 during the spawning run (Table 2.1). The first four tagging dates allowed fish capture from the waters immediately below the dam and fishway, but after the first two weeks of the spawning run, fish were not available in sufficient numbers to be captured with a cast net and were obtained using the weir. Two hundred and fifty one of the fish were implanted with a tag-type that the multireader was able to detect, but due to software conflicts was not able to successfully record the unique tag numbers, and these were therefore excluded from analysis. The remaining 370 tagged fish were used in the analysis of transit time from Macallen Dam to Wiswall Dam (Table 2.1).

At Macallen Dam, 131 of the 370 PIT tagged fish were recorded entering the fishway and 46 of them successfully passed (Table 2.1). Twenty-four of the 46 PIT tagged fish successfully passing the Macallen fishway were detected by the antennas at the Wiswall Dam fishway (Table 2.1). Transit times of Alewives ranged from as short as 4.8 d to as long as 24.1 d, with a mean transit time of 4.8 d (Table 2.1).

Radio Tagging

Ninety-three Alewives were radio tagged from the Wiswall Dam fishway and released at one of three locations (Table 2.2). Seven of the 93 tagged fish were excluded from analysis due to either a lack of detections or erratic movement, which may be attributable to post-release predation (Table 2.3). Within each release location the sex distribution of tagged fish varied, but the distribution of all fish tagged was evenly divided with 47 (51%) males and 46 (49%) females (Table 2.2). Total length of fish tagged ranged from 250 mm to 325 mm with a mean total length of 295.7 mm. The mean total length of females tagged (295.7 mm) was the same as the overall mean of sexes combined, but males had a lower mean total length of 288.1 mm. When comparing means between release locations with ANOVA, the length of fish released at Sites RL (296.2 mm) and BF (294.4 mm) were not significantly different (F= 0.20; df = 1, 67; P = 0.65), but both were significantly larger from those released at Site RR (mean total length of 282.8 mm; F= 5.14; df = 2, 90; P = 0.008; Table 2.2). Samples taken at the head-of-tide Macallen fishway throughout the spawning run indicate that the sex and length distribution of all tagged fish was representative of the river herring population returning to the Lamprey River in 2013 (F= 1.00; df = 1, 391; P = 0.32; Table 2.2).

A total of 3,471,191 detections were recorded during the study period at the six stationary receiver locations, excluding test tags and a 15 minute post-release fish (Table 2.4). Seventy-nine percent of all detections were valid tag detections (including post-release mortality or tag expulsion), followed by signal collision (14.03%), and noise (6.88%; Table 2.4). Half of valid detections were from four fish, tag numbers 12, 16, 63, and 68, which possibly died at the antenna location or expelled their tag at the antenna location (Figures 2.4 through 2.6; Table A.1-–A.3). The remaining 1,328,971 valid detections were used in the analysis of movement within the study area, and their distributions by release site and antenna location are shown in Table 2.4. Most detections (68%) occurred from fish at A3, while antennas A2 and A5 had 12% and 13% of the valid movement detections, respectively. There were no valid detections of tagged fish at antenna A1 throughout the study period.

Due to the close proximity of the four stationary receivers surrounding the Wadleigh Falls Dam location (A1, A2, A3, A4) some overlap among the detection areas (0.1% of the valid detections) and these were corrected in the analysis (Table 2.4). The greatest overlap effect occurred at Antenna 1, where all 118 detections were due to overlap of fish present at either Antenna 2 or 3 (Tables 2.4 and 2.5). In all cases of overlap there was higher recorded signal strength at the antenna included in analysis.

Detailed movements of all tagged fish with post-release detections are shown in Tables A.1 through A.3 and Figures 2.4 through 2.6. All but one of the fish released downriver at BF that continued upriver to Wadleigh Falls selected the river channel leading to the river-right side of the dam (Table 2.3). Total in-river residence time, excluding all fish classified as fallback, exiting the river ranged from 3.3 to 23.1 d post-release. The mean in-river residence time was greatest for fish released at BF, followed by RR and RL, (mean time of 10.4 d), but no differences in residence time among release locations were detected (F= 1.81; df = 2, 45; P = 0.18; Table 2.3).

Fallback (Frank et al. 2009) was exhibited by eighteen fish, 45% of those released at BF, one released at RL, and none released at RR (Table 2.3). Excluding the fish classified as fallback, the length of time spent in the Wadleigh Falls detection area ranged from 0.1 d (85 minutes) for an individual fish to as long as 15.9 d (both for tagged fish released at BF). The mean time fish spent in the detection area was 3.8 d, and there was no difference among release sites (F= 1.79; df = 2, 57; P= 0.18; Table 2.3). Alewife released at RR or RL, immediately below the Wadleigh Falls Dam, spent the greatest amount of time at their respective release sites and fish released downstream at BF spent 87% of their time at A3 (Table 2.6).

TABLE 2.3.—Summary of counts, movements, and in-river residence times for tagged Alewives released at three separate locations in a telemetry study during the 2013 spawning migration in the Lamprey River, New Hampshire.

	Release site			
	River left (RL)	River Right (RR)	Brady Farm (BF)	All sites
Total released:	24	24	45	93
Number used in analysis:	22	24	40	86
Number of fallback:	1	0	18	19
Number detected exiting the river:	13	23	30	66
Time in Wadleigh Falls detection area (d):				
Mean	3.4 d	3.3 d	5.2 d	3.8 d
Min	0.2 d	0.2 d	0.1 d	0.1 d
Max	13.1 d	8.7 d	15.9 d	15.9 d
River channel selected:				
RL	-	-	1	1
RR	-	-	21	21
Movement from Wadleigh Falls to Wiswall Dam[1]:				
Mean time elapsed	1.6 d	1.3 d	1.4 d	1.4 d
Mean speed (rkm/hr)	0.33	0.42	0.039	0.38
Max speed (rkm/hr)	2.03	6.30	6.14	6.30
Movement from Wiswall Dam to Macallen Dam[1]:				
Mean time elapsed	1.3 d	1.2 d	1 d	1.1 d
Mean speed (rkm/hr)	0.18	0.2	0.23	0.21
Max speed (rkm/hr)	1.20	1.29	1.95	1.95
Total time in river[2]:				
Mean	8.8d	10.9 d	11.1 d	10.4 d
Min	4.2 d	4.2 d	3.3 d	3.3 d
Max	20.2 d	16.2 d	23.1 d	23.1 d

[1] Including fish classified as fallback; [2] Excluding fish classified as fallback.

TABLE 2.4.—Count of detection records within each classification category after data processing of radio tagged Alewives for a telemetry study during the 2013 spawning migration in the Lamprey River, New Hampshire.

Detection classification	Number of detections	%	Used in analysis
Valid: dead at antenna	1,407,080	40.54%	No
Valid: movement detections	1,328,971	38.29%	Yes
Signal collision	486,996	14.03%	No
Noise	238,833	6.88%	No
Wrong channel	5,552	0.16%	No
Invalid tag number	2,324	0.07%	No
Unexplained	1,435	0.04%	No
Total	3,471,191		

TABLE 2.5.—Number and percentage of detections and overlapping detections recorded for radio tagged Alewives for a telemetry study during the 2013 spawning migration in the Lamprey River, New Hampshire.

		Overlap detections at each antenna (not included in analysis)					
Antenna	Valid detections	A1	A2	A3	A4	A5	A6
A1	0	-	117 (99%)	1 (1%)	-	-	-
A2	174,848	-	-	8 (< 1%)	4 (< 1%)	-	-
A3	906,408	-	851 (< 1%)	-	114 (< 1%)	-	-
A4	7,125	-	-	239 (3%)	-	-	-
A5	165,868	-	-	-	-	-	-
A6	73,388	-	-	-	-	-	-
Total	1,327,637	0	968 (0.07%)	248 (0.02%)	118 (0.01%)	0	0

The calculated mean speed of downriver movement for fish classified as fallbacks was not different from those moving upstream (Table 2.3) and therefore all fish that were detected at Wiswall Dam after release were used to calculate the mean speed by release site and overall (Table 2.3). Sixty-six (77%) of the 86 tagged fish used in the analysis were detected exiting the river at the Macallen Dam (Table 2.3).

TABLE 2.6.—Time spent at each antenna location by fish released at three separate locations in the Lamprey River, New Hampshire.

	Antenna locations						
	A1	A2	A3	A4	A5	A6	
Release site	Hours (%)	Hours (%)	Hours (%)	Hours (%)	Hours (%)	Hours (%)	Total hours
River Left (RL)	0 (0%)	90,971 (42%)	50,497 (23%)	1,979 1%)	67,573 (31%)	4,896 (2%)	215,916
River Right (RR)	0 (0%)	0 (0%)	107,303 (85%)	447 (<1%)	16,593 (13%)	2,389 (2%)	126,732
Brady Farm (BF)	0 (0%)	6,075 (5%)	105,348 (87%)	592 (<1%)	7,565 (6%)	1,144 (1%)	120,724
Total hours at antenna	0 (0%)	97,046 (21%)	263,148 (57%)	3,018 (1%)	91,731 (20%)	8,429 (2%)	463,372

Discussion

With the opening of the new fishway at the Wiswall Dam on the Lamprey River in 2012, river herring were observed migrating and congregating as far as 21.4 km upriver from the Wadleigh Falls Dam. Prior to this, it was unknown if river herring were able to pass the remaining breached dam structure, since they were not able to migrate beyond the Wiswall Dam at rkm 12.8. Field observations of river herring unable to pass this location in 2012 and 2013 were confirmed in this radio tagging study.

To be confident in these results, it was important to ensure that the inability of Alewife to pass the barrier was due to the barrier itself and stream conditions, and not a result of mortality or behavioral changes due to tagging and handling stress. The tagging procedure used was similar to that described by Smith et al. (2009), which demonstrated that the tagging protocol had low impacts on river herring movement and behavior. Post-release movements of fish in-river were examined to determine if fish behavior appeared to be representative of a typical Alewife's attempt at upstream migration during the spawning run. Fallback is one type of observed behavior described in previous tagging studies of tagged alosines (Barry and Kynard, 1986; Monk et al.

1989; Beasley and Hightower, 2000; Hightower and Sparks, 2003; Bailey et al. 2004; Sprankle, 2005; Olney et al. 2006; Frank et al. 2009). Quantification and classification of this tag-effect has varied (Frank et al. 2009) among the previous studies, but can generally be described as immediate or continued downstream movement following tagging of a fish which was captured during the upstream migration. Nineteen of the tagged fish in this study were classified as fallbacks (Tables 2.6 and 2.7) and were primarily of fish released at BF. Comparing the in-river movements of fallbacks (e.g., tag #'s 12, 80, 37, 89, and 94) , shown in Figures 2.4 through 2.6, to the movements of other tagged fish present at Wadleigh Falls, a directed and continued downward movement is evident even though some of the fish did make an initial 1.4 km movement upstream from the BF release site. Therefore, fallbacks were not used in the analysis to determine the mean time a tagged fish remained at receiver location or to calculate the mean total time a tagged fish remained in the river after being released. Similarly, fish were excluded from analysis if they likely died post-tagging or expelled their tag post-release. While this study did not conduct a separate tagging mortality study, the fact that 66 of the 86 tagged fish (77%) were detected in the Lamprey River suggests that the mortality rate associated with radio tagging was low (Table 2.3).

Using measurements of in-river time and length of time at Wadleigh Falls post-release, as indicators of fish behavior, suggests that tagged fish, excluding fallbacks, exhibited behavior similar to that expected for non-tagged fish. The mean time a fish remained within the detection area of the receivers at Wadleigh Falls was 3.8 d and the mean total time in-river post-release was 10.4 d (Table 2.3). The total in-river residence time is similar to the length of time tagged Alewives remained upriver (9.5 d) as reported by Smith et al. (2009) in the Nemasket and Ipswich Rivers in northeastern Massachusetts. Also, since Alewives were captured at the Wiswall Dam for tagging, the mean transit time of 4.8 d (Table 2.1) from the PIT tagged fish should be added to the total post-release in-river time. Therefore the total residence time between entrance and exit at the head-of-tide dam was 15.2 d, which is shorter, but similar to the median residence time observed for Alewives in Lower Guilford Lake, Connecticut (16.5 d; Franklin et al. 2012). Residence times of the current study indicate that, on average, more than one-third of the entire time a tagged fish spent in the river post-release was spent at the base of Wadleigh Falls Dam. The residence time, as well as field observations of fish, both tagged and untagged, that were seen congregating in the area for several days during the study period, suggests that the tagged fish used in the analysis exhibited typical migratory behavior. The prolonged length of time spent at the Wadleigh Falls location, observations of unsuccessful attempts to ascend the ledge and deposition of eggs on the cobble substrate in the areas immediately below the breached dam indicate that Alewives will spawn below dams if unsuccessfully ascended. This is likely a less than ideal location, since previous research on the spawning behavior of Alewives indicates that spawning usually occurs in quiet waters of ponds and coves and in sluggish stretches of streams above the head of tide, rather than in the flowing sections of the run of the river that are preferred by Blueback Herring (Loesch 1987; Loesch and Lund 1977; Collette and Klein-MacPhee 2002). An island approximately 0.3 km below the Wadleigh Falls Dam location divides the Lamprey River into two distinct and physically divided river channels (Figure 2.2). If restoration efforts were made at that location in an effort to allow river herring the ability to pass this barrier, it may be important to know which route that they would choose to continue their migration. Of the 45 fish released at BF, 22 of them continued their migration up river to Wadleigh Falls and 21 (95%) of those tagged fish selected the channel on river-right where A3 was located (Table 2.3 and Figure 2.2). Additionally, of the 21 fish released at RL that did not fallback, four (19%) of them moved downriver from RL, were detected at the split by A4, moved back upriver, and were detected on river-right by A3

(Table 2.5). However, none of the fish released at RR and only three (14%) of those released at BF and moved upriver were ever detected by A2 in the river-left channel (Table 2.5). These movements show that once a tagged fish arrived at the Wadleigh Falls Dam location, that this study found was an impassable barrier, they made little exploratory movements downriver to search for another route. The factors that may contribute to determining channel selection were not part of this study, however, as shown by the river discharge levels in Figures 2.4, 2.5, and 2.6 the flows remained fairly constant at low levels during the study period and only increased at about the time the last tagged fish were exiting the river. The depth of the river channel on river-left is considerably shallower than river-right, which during periods of lower river discharge may result in higher water temperatures, a reduced number of temperature relief areas in deeper pools, and may be difficult for large schools of migrating herring to negotiate as easily.

While field observations did note greater numbers of river herring over a longer period of time on river-right than river-left, with only minor modifications to the breached dam structure river-left may provide passage more easily and with flow conditions not experienced during this study. River herring were observed on river-left swimming into the falls created by the remaining keyway structure of the former dam and were very close to successfully ascending the falls. Also, overlap detection data that were obtained during the study on A1 above the dam were from fish which were actually present in the detection area of A2 (Table 2.5). It is very likely that when fish attempted to pass the barrier and approached the impoundment area behind the dam that their signals would be detected by A1 even though the fish was not able to pass. These findings should be taken into consideration in the future if efforts are conducted to restore fish passage at Wadleigh Falls for Alewives and other resident fish. While passage may be more easily provided with less modification to the river-left section of the dam, the low numbers of fish choosing that path suggest that greater numbers of fish would pass on river-right.

In conclusion, 623 Alewives were PIT tagged and 93 were radio tagged in the Lamprey River during the 2013 spawning migration. Comparing the sex and length distributions of tagged fish to those taken at the head-of-tide fishway throughout the migration, indicates that the tagged fish were representative of the general population in the river. Alewives PIT tagged at the first two fishways on the river were used to estimate the mean transit time of fish that continued their upstream migration as far as the Wiswall Dam. Eighty-six (92%) of the tagged fish were detected throughout the spawning migration and provided information useful in the analysis of in-river movements and passage of the breached dam. Nineteen of the fish exhibited a fallback behavior, but the remaining 67 fish either remained in the area or continued their upriver migration to Wadleigh Falls. Data from movements of the tagged fish which did not fallback were typical of spawning migration behavior. Receiver detections indicate that none of the fish, released immediately below Wadleigh Falls or those released 1.1 km downriver, were able to pass the barrier and continue upstream. Data showed that 95% of fish selected the river-right channel as they migrated upriver and that few exhibited exploratory behavior, switching from one river channel to another. Finally, field observations throughout the study indicated that river herring attempted to pass on each side of the river, but vast majority selected river-right. Unfortunately, this branch, because of discharge volume and river depth, would require considerably more modification to permit river herring passage than river-left.

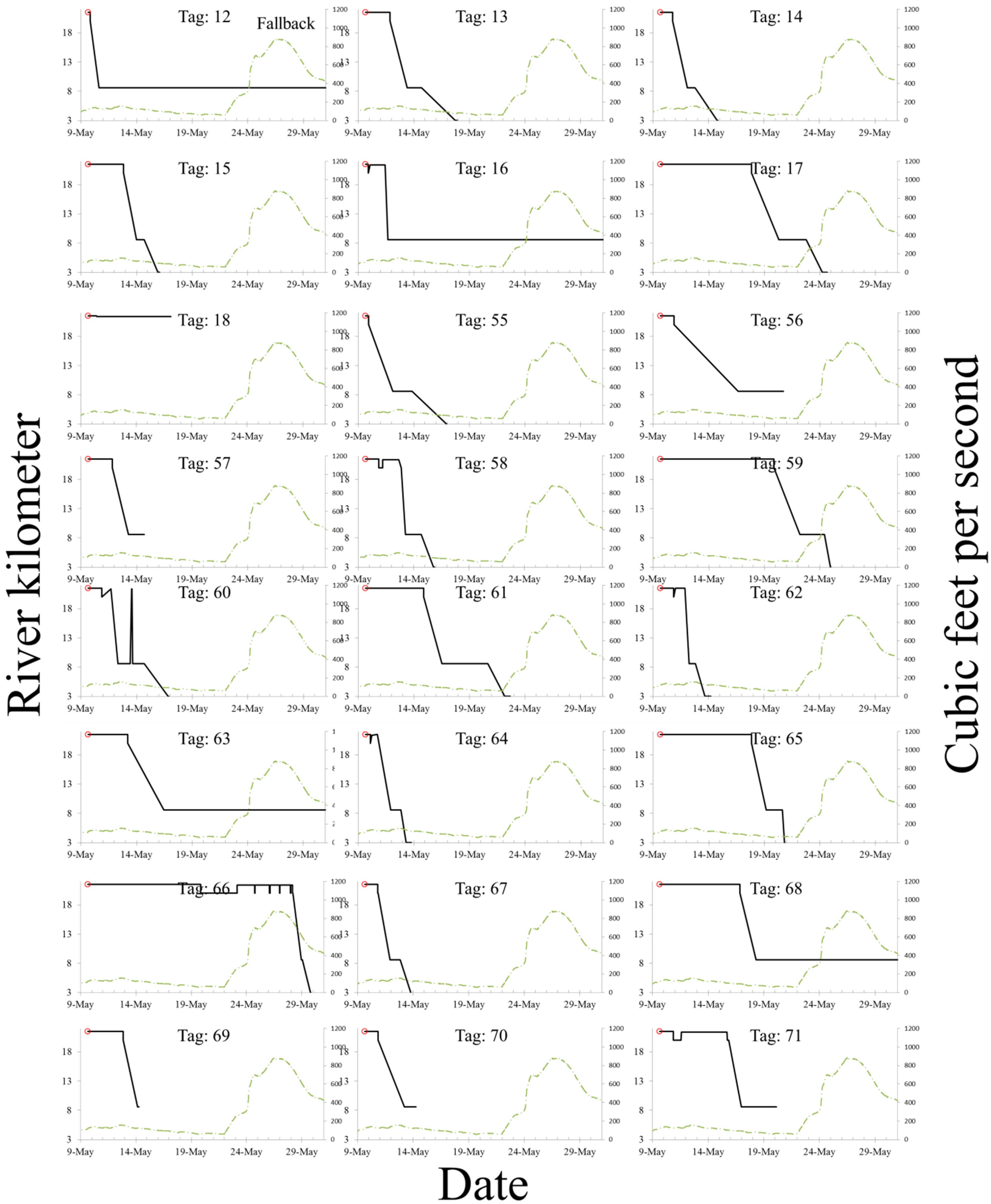

FIGURE 2.4.—Movements of tagged Alewives released at river-left side of Wadleigh Falls Dam (RL). Circle indicates time and river kilometer of release, solid line indicates fish detections, dashed line indicates river discharge.

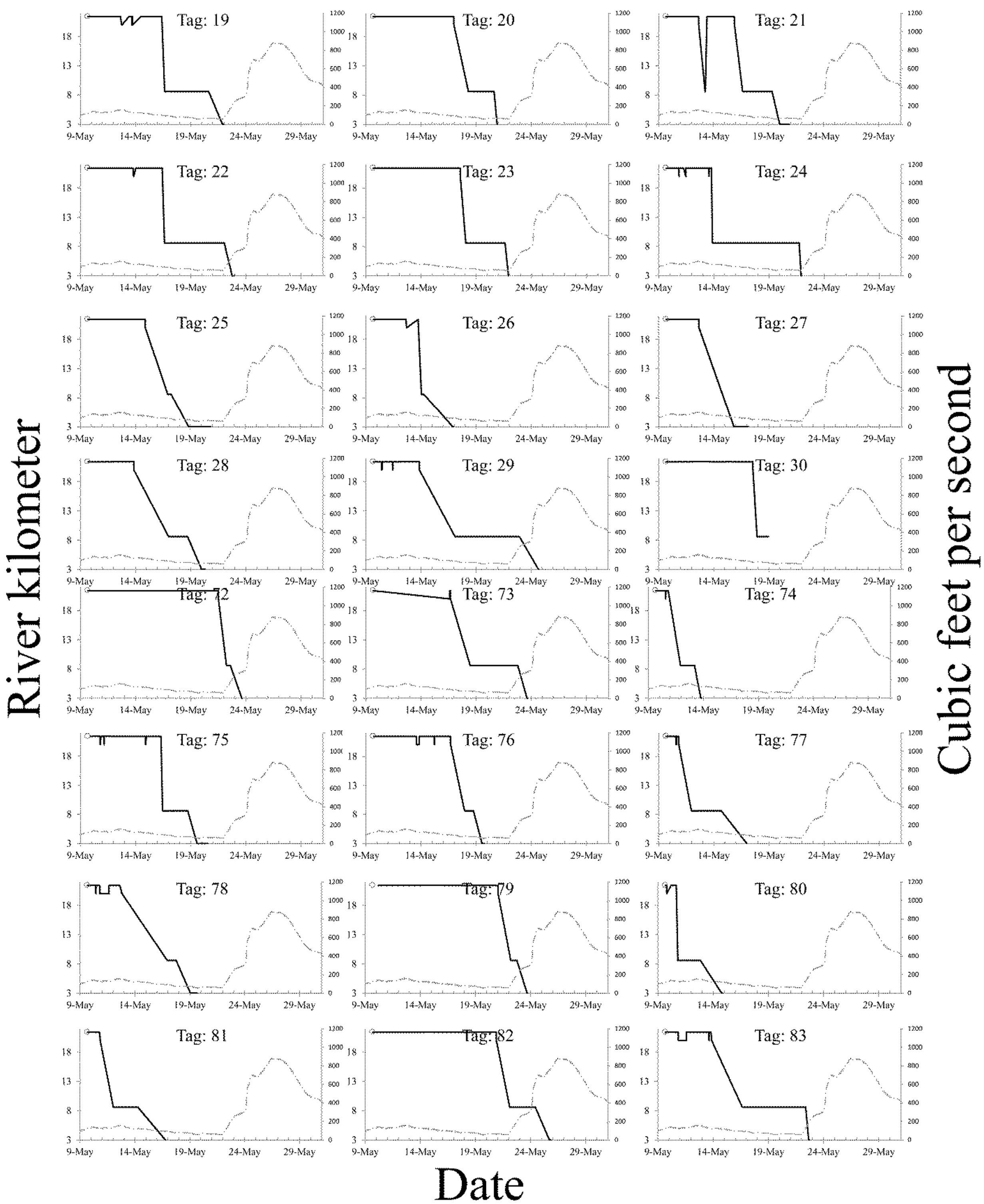

FIGURE 2.5.—Movements of tagged Alewives released at river-right side of Wadleigh Falls Dam (RR). Circle indicates time and river kilometer of release, solid line indicates fish detections, dashed line indicates river discharge.

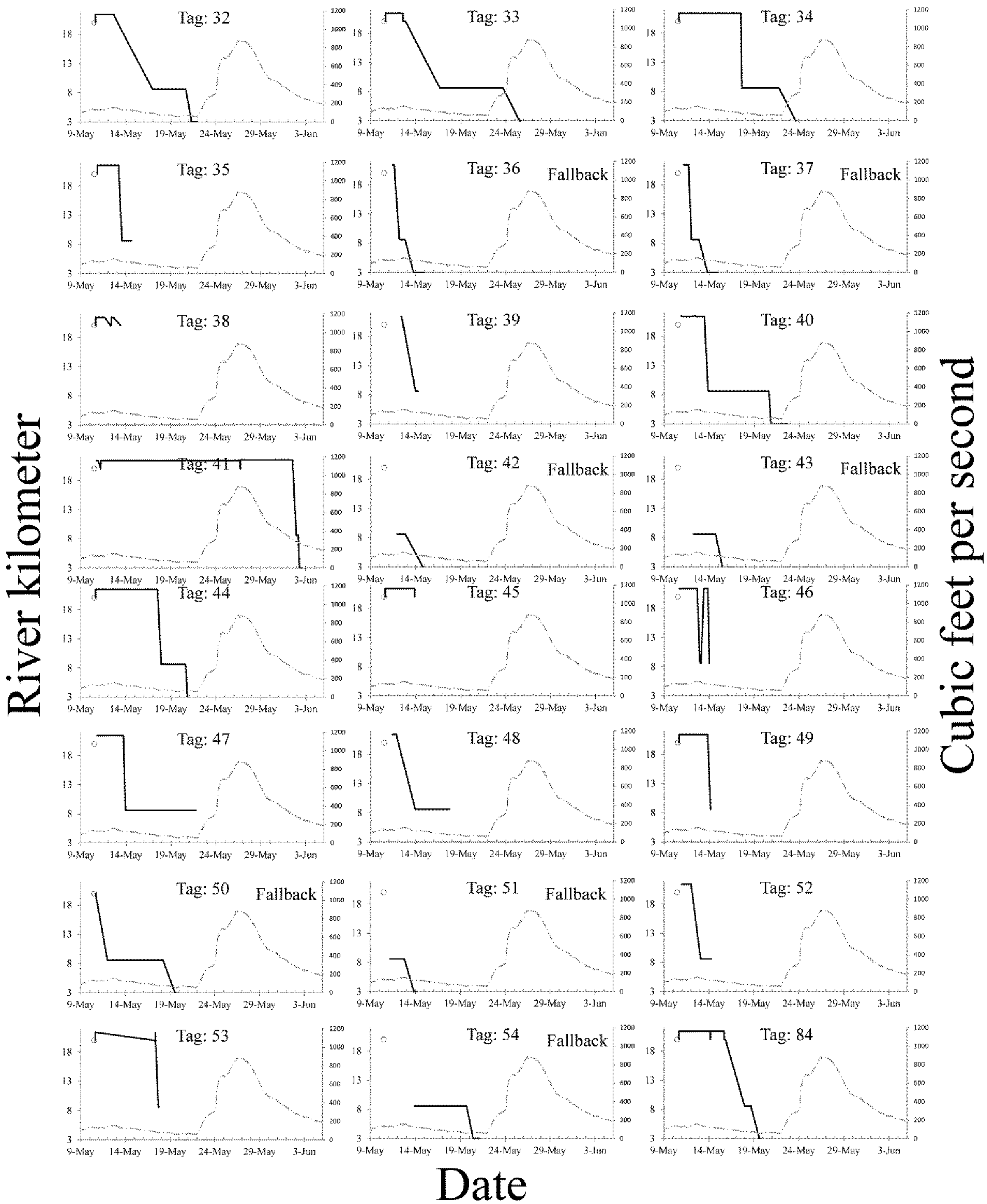

FIGURE 2.6.—Movements of tagged Alewives released at Brady Farm (BF). Circle indicates time and river kilometer of release, solid line indicates fish detections, dashed line indicates river discharge.

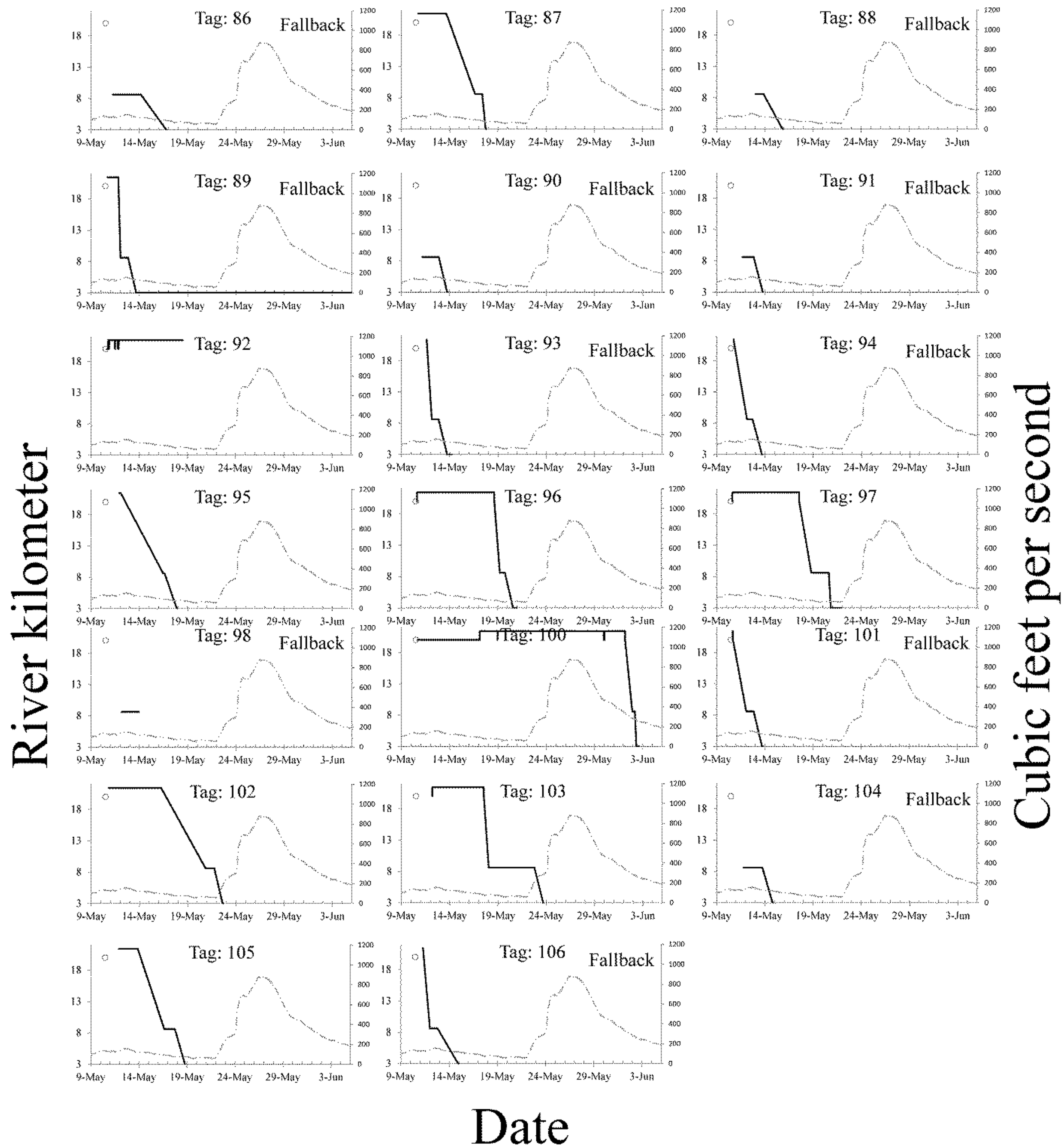

FIGURE 2.6.—(CONTINUED)

CHAPTER 3

DIGITAL IMAGE ANALYSIS AS A TECHNIQUE FOR ALEWIFE (*ALOSA PSEUDOHARENGUS*) FECUNDITY ESTIMATION

Introduction

Alewife (*Alosa pseudoharengus)* and Blueback Herring (*A. aestivalis)*, collectively referred to as river herring, are sympatric throughout much of their range, and because of similarities in appearance and life history characteristics, are jointly managed (Richkus and DiNardo 1984; Loesch 1987). Both species exhibited dramatic population declines over their entire range in recent years and were listed as a "species of concern" by the National Oceanic and Atmospheric Administration (NOAA) in 2006 (Limburg and Waldman 2009; ASMFC 2012). Anadromous Alewives undertake vernal spawning migrations to their natal spawning grounds, but dams constructed over the past centuries often restrict their movements (Collette and Klein-MacPhee 2002).

Fecundity estimates are important in fisheries management to determine the reproductive potential of mature fish in a population, for predicting trends in species abundance, and measuring spawning stock biomass (Nitschke et al. 2001). Previous studies found that Alewife are highly fecund (≤ 456,700 oocytes/ female), fecundity varies by latitude, and that all of the fully developed oocytes may not be ovulated during a spawning season (Kissil 1974; Loesch and Lund 1977; Jessop 1993).

In this study, two methods for determining Alewife fecundity were compared from fish captured during their annual spawning migrations.

Methods

Ovary collection.— Alewives were collected from the trap associated with a fish ladder at the Macallen Dam (Newmarket, New Hampshire) between April 25 and May 17, 2012. The dam is located at the head of tide and is the first barrier to Alewife passage during vernal spawning migrations. Based on previous sampling data, a length distribution of 24–34 cm (total length) was expected, and during the sampling period an effort was made to collect up to ten mature female fish per 1-cm bin. Females were identified visually by enlarged ventral areas, and collected fish were immediately placed on ice and sampled within twenty-four hours. The fish were measured (TL ±1mm) using a measuring board and weighed (± 0.1 g) with a digital balance. A scale sample was removed from the left dorsal area above the lateral line and immediately below the dorsal fin. The ovaries were removed, weighed individually (± 0.0001 g), and the left ovary was immediately placed in Gilson’s solution, to harden the oocytes and dissolve the ovarian tissue (Bagenal and Braum 1971). The right ovary was further sub-sampled, as described below.

Scale aging.— Scales were placed in plastic centrifuge tubes, filled with a solution of pancreatin (4,000 ppm) and agitated with a sonicator to remove the mucous membrane that can obscure annuli (Enterline 2013). At least eight clean scales were mounted between glass microscope slides and aged independently by two readers using the methods described by Marcy (1969). Images of the scales were recorded with a digital video camera mounted atop a dissecting microscope using the image analysis program Image-Pro V6.2.

Gonadosomatic index.—To ensure that spawning had not begun before the sampling period, fish were collected throughout the length of the spawning season to measure in-season ovary weights. Gonadosomatic index were calculated for each fish (Snyder 1983; Wooton 1990; Dee and Parrish 1994; Nitschke et al. 2001) using the following equation:

$$GSI = \frac{OW}{SW} \times 100 \tag{1}$$

where SW is somatic weight (g) and OW is total ovary weight (g). Somatic weights were wet weights of eviscerated females. Up to five mature females of each 1-cm bin were collected and sampled weekly when present, until Alewife were no longer observed passing at the fish ladder. A correlation analysis was used to examine GSI in relation to collection date, TL, and SW. An ANOVA was done to compare GSI means between all sample weeks and each 1-cm bin.

Estimation of fecundity and comparison of techniques

Gilson's solution treatment (left ovary).— Each left ovary remained in Gilson's solution for at least one year. Samples were shaken daily for the first week of storage and periodically thereafter. Fecundity was estimated gravimetrically (Bagenal and Braum 1971; Bagenal 1978) as it is considered more precise than the volumetric method (Snyder 1983). Gilson's solution was drained using vacuum filtration and oocyte samples weighed (± 0.001 g). Three subsamples (0.029 to 0.050 g) of the oocytes were weighed and counted visually using a dissecting microscope. The mean of the three subsamples were used to estimate the total fecundity —the count of all oocytes present, including those not likely to be mature at time of spawning— using the methods of Griswold and Silverman (1992) and Jessop (1993) as follows:

$$Total\_Fecundity = mean\left(\frac{subsample\_count\_of\_eggs}{subsample\_weight}\right) \times OW \qquad (2)$$

where OW is the total ovary weight (g).

Longitudinal subsampling and image analysis (right ovary).— The right ovary was visually divided into three equal longitudinal sections: anterior, center, posterior (Figure 3.1). A 1 cc syringe was used to aspirate a subsample of oocytes (0.0988 to 0.1713 g) through the ovarian

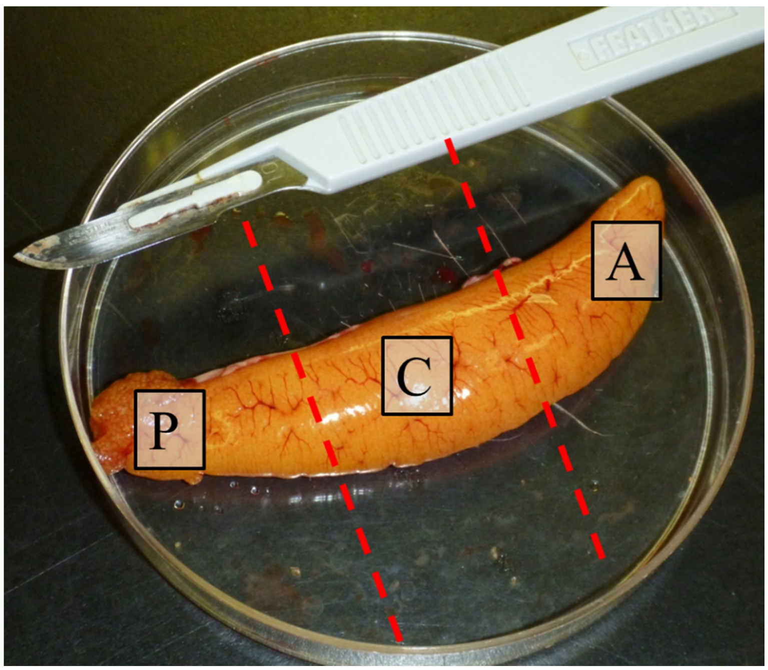

FIGURE 3.1.— Ovary sample removed from a mature adult female Alewife sampled during the 2012 vernal spawning run from the Lamprey River, Newmarket, New Hampshire. Ovary sample locations are shown as A =anterior, C = center, P = posterior

wall from each section of the ovary. The samples were fixed in 10% phosphate buffered formalin for six weeks during which they were shaken periodically. After six weeks, the formalin was removed with a transfer pipette and samples were poured into a 100 x 15 mm petri dish, covered with 70% ethanol. The petri dish was covered with a black-painted lid to provide a contrasting background. Petri dishes were scanned using a flatbed scanner (Epson Perfection V500 Photo, Epson America, Long Beach, CA), capturing images at a resolution of 1,200 dots per inch in 8-bit grey scale and saved in uncompressed tagged image file format (.TIFF; ~ 27 MB; Figure 3.2A). Scanned images were analyzed using ImageJ Version 1.34j (National Institutes of Health, Bethesda, Maryland) image analysis software with an oocytes macro. An image analysis procedure, similar to that outlined by Thorsen and Kjesbu (2001) and McCarthy et al. (2008), was used (Figures 3.2B–2C) with a roundness threshold of 0.8 to remove unwanted particles. An oocyte diameter range (100–1,200 μm), was set to reduce the number of clustered oocytes incorrectly measured as a single oocyte (Jessop 1993) and all diameters were measured (± 1μm) by the software (Figure 3.2D). All images were reviewed visually to remove misidentified objects such as ovarian tissue and clumps of oocytes and to count and measure oocytes that were not identified by the computer analysis.

Distributions of oocyte diameters from each ovary section were pooled for all fish within each 1-cm bin and plotted to check for homogenous distribution along the length of the ovary. Three fecundity estimates per fish were calculated gravimetrically (Bagenal and Braum 1971; Bagenal 1978), one for each ovary section (anterior, center, posterior). Subsample counts were extrapolated to estimate the total number of oocytes in the entire ovary as follows:

$$Subsample\_fecundity = \left(\frac{subsample\_count\_of\_eggs}{subsample\_weight} \right) \times OW \qquad (3)$$

where OW is the total ovary weight (g). Subsample fecundity estimates for each ovary section were compared for differences within each 1-cm bin using ANOVA. If the subsample fecundity estimates were not significantly different for all three ovary sample locations within a bin, total fecundity of each Alewife was calculated using equation (2).

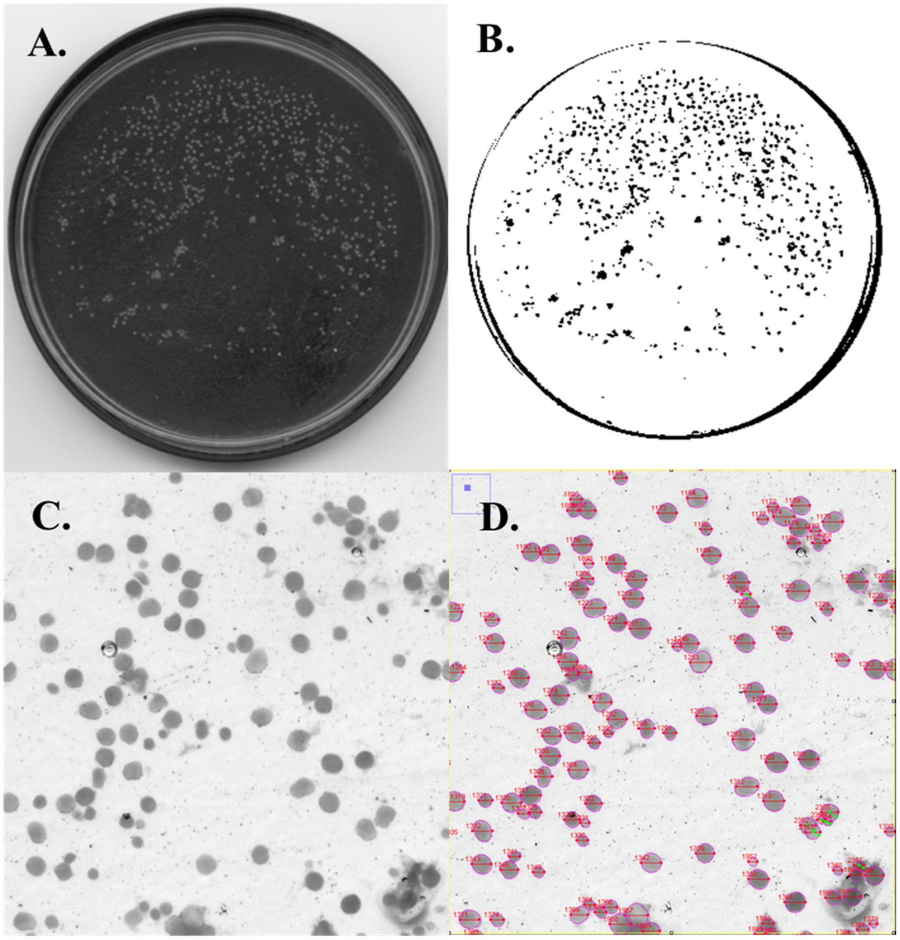

FIGURE 3.2.— Scanned images of (A) a full subsample from a single ovary section and (B) the image after first stages of image processing where the image is inverted to negative, the outside is cleared, and converted to black and white. (C) A zoomed in view of the oocytes that ImageJ analyzed, and (D) the resulting analysis with eggs outlined in red, each numbered individually, and a line across the diameter measurement.

The estimates of total fecundity produced by both techniques (i.e., Gilson's solution, image analysis) were compared for differences using Student's t-tests. Three fecundity relationships were examined with a simple linear regression, TL-total fecundity, SW-total fecundity, and age-total fecundity. All data were $\log_{10}$ transformed to meet statistical assumptions (e.g., normality of residuals).

Results

Ovary collection

Alewives first appeared at the Macallen Dam on April 16, 2012 and continued to pass in pulses of fish for a six week period until May 29. Ovary collections began on the ninth day of the spawning migration and continued over five weeks through the last day when fish were present. Alewives collected for *GSI* (N = 172) and estimation of fecundity (N = 69), ranged from 24.0 to 34.3 cm, with a mean of 29.4 cm. Total lengths of sampled female Alewife were compared to length data collected from those returning to the fishway between 2001 and 2011 (N = 2,025; mean = 29.4 cm; SD = 1.87; M. Dionne, New Hampshire Fish and Game Department, unpublished data; Figure 3.3A). The number of fish sampled in each bin is shown in Figure 3.3B. Ten fish were sampled for bins 27, 29, 30 and 32-cm, and 9, 8, and 7 fish were sampled for the 31, 28, and 26-cm bins, respectively. Only 2 fish were sampled for the 24 and 25-cm bins and 1 for the 34-cm bin. No fish were sampled for the 33-cm bin (Figure 3.3B). Eighty-four percent of fish sampled for fecundity were collected the first two weeks of the spawning run, and the remaining 11 samples were collected the third week. Somatic weights of Alewives sampled ranged from 135.7 to 367.0 g with a mean of 249.4 g.

Gonadosomatic index

Alewife GSI of the 172 fish sampled over the five sampling weeks varied from 4.19 to 16.22 (mean = 9.70; SD = 1.60; N = 172), and GSIs of Alewife used for fecundity estimation ranged from 5.85 to 16.22 (mean = 9.50; SD = 1.79; N = 69). There were no significant correlations found between GSI and date of collection (r = 0.106; N = 172; P = 0.17; Figure 3.4A), TL (r = 0.090; N = 172; P = 0.24; Figure 3.4B), or SW (r = 0.107; N = 172; P = 0.16;

Figure 3.4C). Furthermore, no differences were found in ANOVA comparisons of GSI between all sampled weeks (F= 1.14; df = 4, 167; P = 0.34) or between 1-cm bins (F= 0.88; df = 9, 162; P = 0.54).

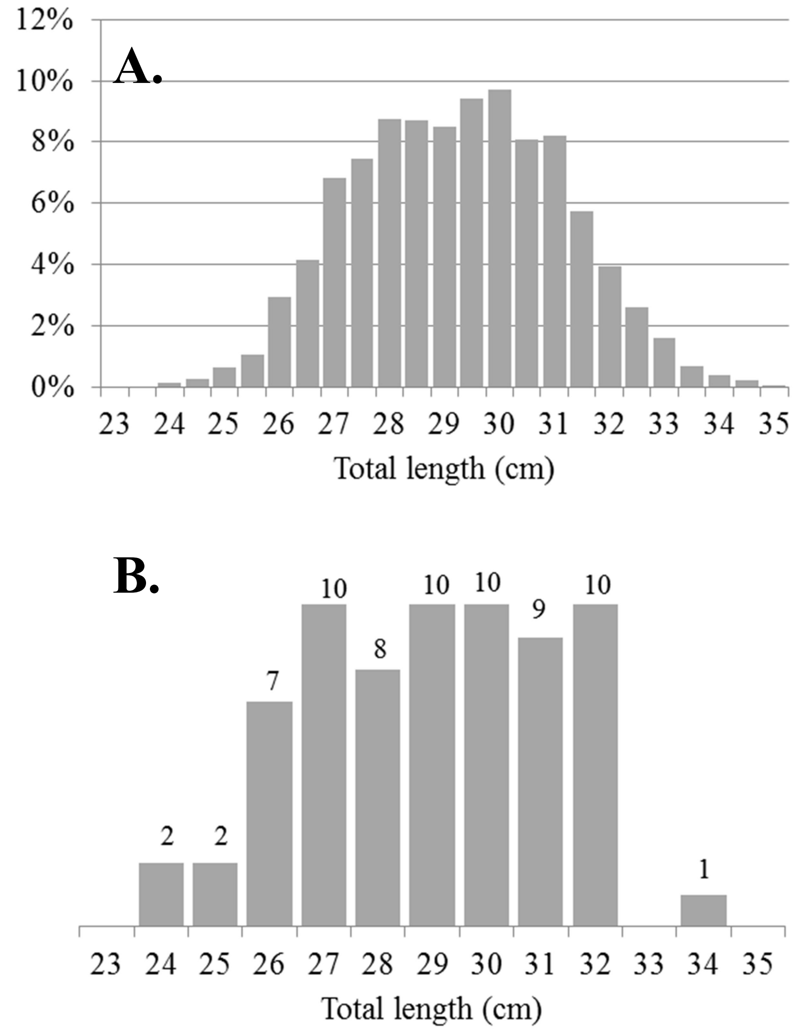

FIGURE 3.3.— Distributions of (A) total length of mature female Alewives returning to the Lamprey River fish ladder at the Macallen Dam on the Lamprey River, Newmarket, New Hampshire between 2001 and 2011 (N = 2,025; mean = 29.4 cm; SD = 1.87; M. Dionne, New Hampshire Fish and Game Department, unpublished data) and (B) number of mature adult Alewives sampled for fecundity estimation (N = 69).

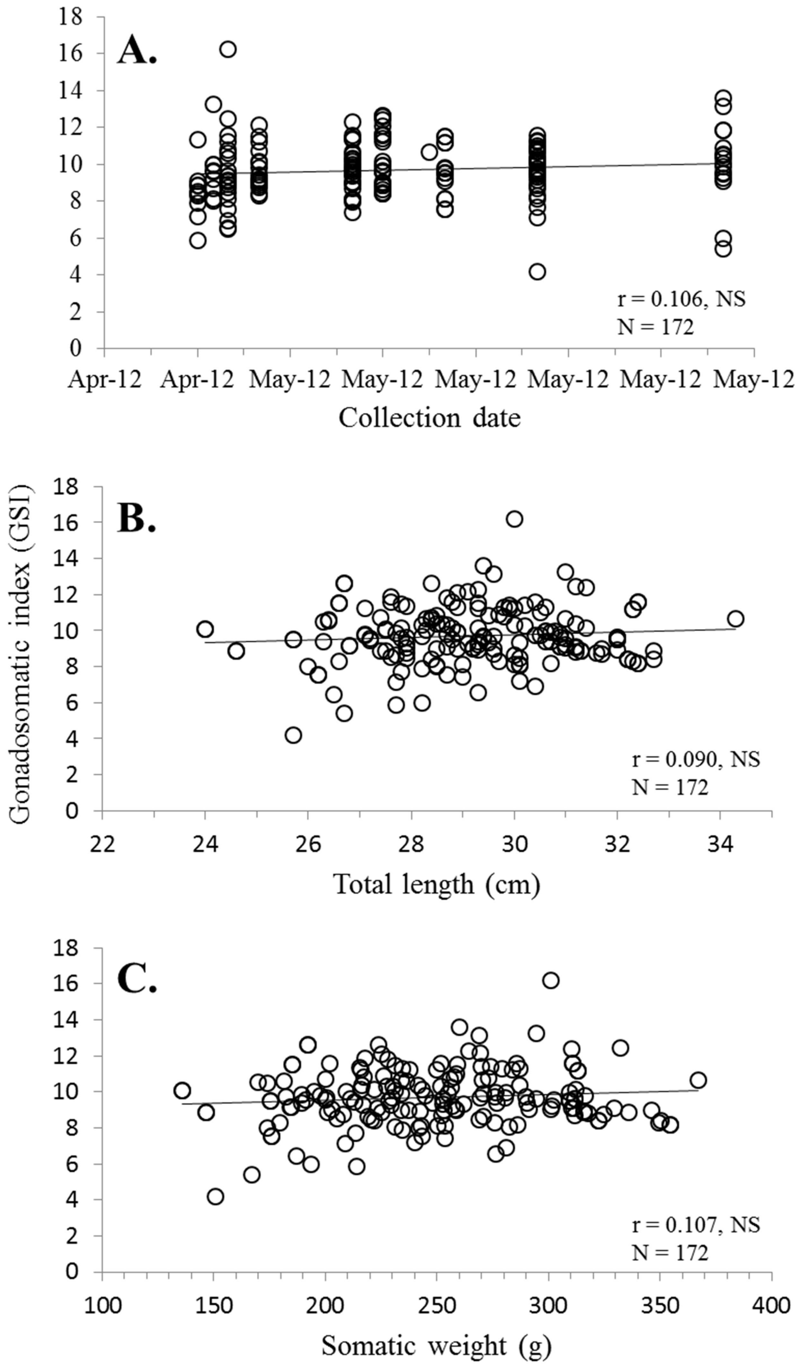

FIGURE 3.4.—Correlation analysis between gonadosomatic index and (A) collection date, (B) total length, and (C) somatic weight for Alewife collected in Lamprey River, New Hampshire. NS signifies no significant relationship.

Estimation of fecundity

Longitudinal subsampling and image analysis (right ovary)—Oocyte diameter distributions by ovary section were plotted for each 1-cm bin (Figure 3.5). Comparisons showed similar diameters across all three ovary sampling locations within each 1-cm bin. A bimodal distribution, with peaks at approximately 400µm and 750µm, was found for all bins and ovary sections (Figure 3.5).

Total fecundity estimates by ovary section ranged from 100,400 oocytes in the center ovary section of 26-cm bin to 408,500 oocytes in the center section of the 32-cm bin (Table 3.1). No differences were found in fecundity estimates across ovary sections within each bin (Table 3.1; Figure 3.6). A means comparison was not possible for the 34-cm bin because only one fish was collected. As no difference in fecundity estimates among ovary sections were found, a single estimate of total fecundity was calculated using the mean of all ovary section subsamples. Estimates of total fecundity using image analysis ranged from 130,200 oocytes for the 25-cm bin to 332,500 oocytes for the 34-cm bin (Table 3.2). Alewife total fecundity generally increased with length over the range of bins.

Gilson's solution treatment (left ovary).—Total fecundity estimates for ovaries stored in Gilson's solution were calculated for 71 fish and a mean estimate was calculated for each bin. Total fecundity estimates using this technique ranged from 121,000 oocytes for the 25-cm bin to 364,900 oocytes for the 34-cm bin (Table 3.2). As with the estimates generated by image analysis, Alewife fecundity also increased with length over the range of bins.

TABLE 3.1.—Estimated total fecundity of Alewives using image analysis for each ovary sampling location by 1-cm bin and ANOVA results for comparisons within bins. NS indicates no significant difference. NP indicates that due to sample size it was not possible to conduct ANOVA.

TL bin	Ovary section	Estimated total fecundity (Thousands of eggs)				ANOVA			
		Mean	SE	Min	Max	F	P	Sig/NS	N
24-cm	Anterior	159.4	22.4	137.0	181.7	0.552	0.625	NS	2
	Center	148.1	5.4	142.7	153.4				
	Posterior	134.9	17.0	117.9	151.8				
25-cm	Anterior	137.3	29.1	108.2	166.4	0.112	0.898	NS	2
	Center	132.2	31.8	100.4	163.9				
	Posterior	121.0	3.4	117.6	124.4				
26-cm	Anterior	161.7	15.3	117.2	232.0	0.043	0.958	NS	7
	Center	156.1	17.6	113.9	231.0				
	Posterior	155.9	14.4	118.2	211.6				
27-cm	Anterior	212.3	15.9	171.6	310.3	1.070	0.359	NS	9
	Center	194.7	17.3	152.6	313.7				
	Posterior	179.6	14.2	127.7	272.5				
28-cm	Anterior	218.9	19.4	145.6	327.2	0.189	0.829	NS	8
	Center	207.2	19.6	135.7	286.4				
	Posterior	203.7	15.3	144.0	255.5				
29-cm	Anterior	236.7	18.5	148.9	330.8	0.277	0.760	NS	10
	Center	243.2	17.7	173.1	345.3				
	Posterior	225.0	16.4	158.4	312.6				
30-cm	Anterior	221.1	16.8	129.6	301.1	0.382	0.686	NS	10
	Center	236.6	20.0	148.1	336.4				
	Posterior	214.8	17.5	150.1	312.5				
31-cm	Anterior	299.8	11.1	243.4	344.1	0.391	0.680	NS	10
	Center	307.7	17.5	175.5	382.0				
	Posterior	282.1	13.7	188.7	360.1				
32-cm	Anterior	306.6	16.4	221.3	407.7	0.406	0.670	NS	10
	Center	297.1	22.9	219.7	408.5				
	Posterior	321.3	17.3	234.5	385.6				
34-cm	Anterior	369.6	-	369.6	369.6	NP	NP	NP	1
	Center	330.3	-	330.3	330.3				
	Posterior	297.5	-	297.5	297.5				

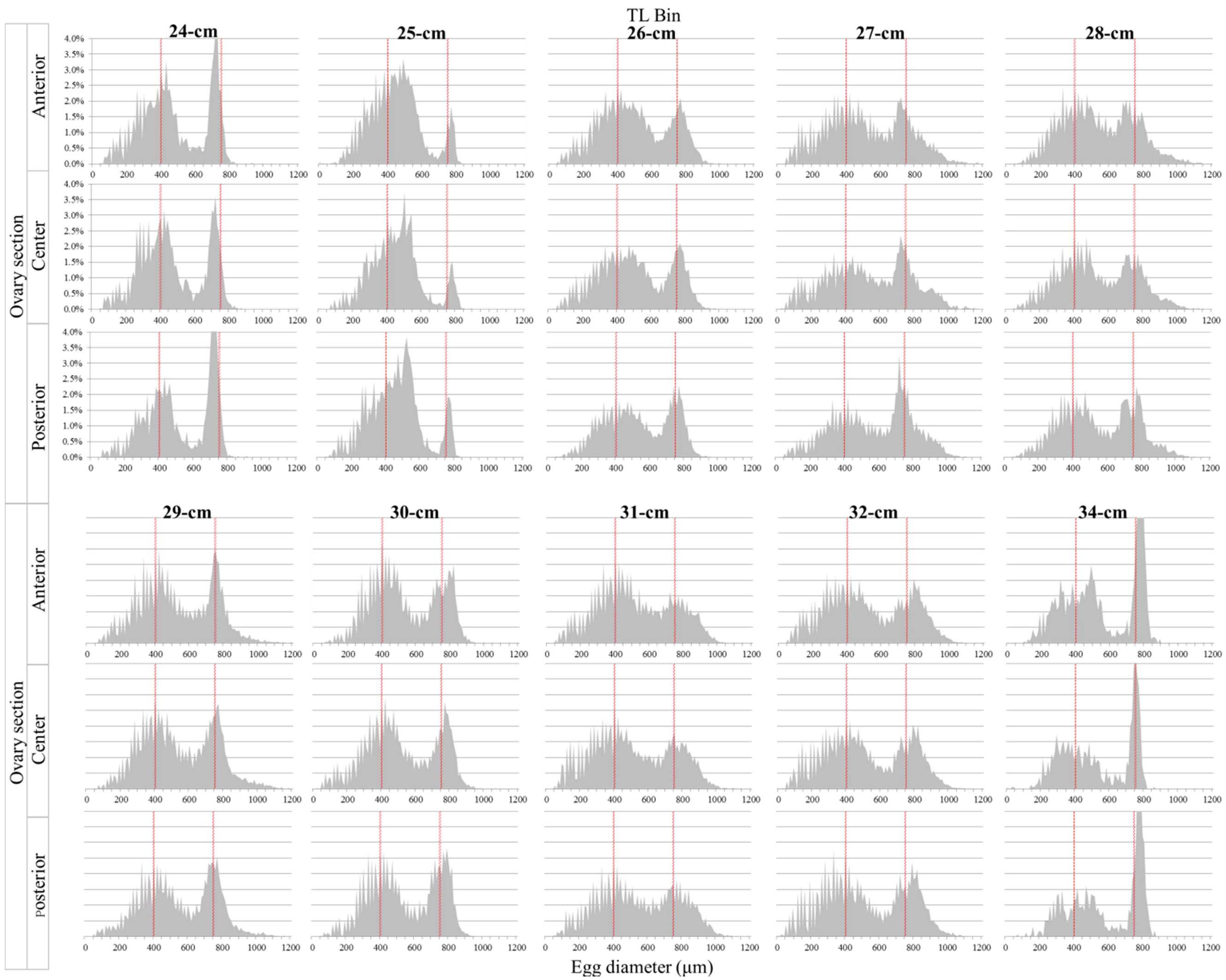

FIGURE 3.5.— Distribution of egg diameters by ovary sample location (anterior, center, posterior) for Alewives collected in Lamprey River, Newmarket, New Hampshire within each 1-cm bin. Dashed lines represent diameters of 400 µm and 750 µm.

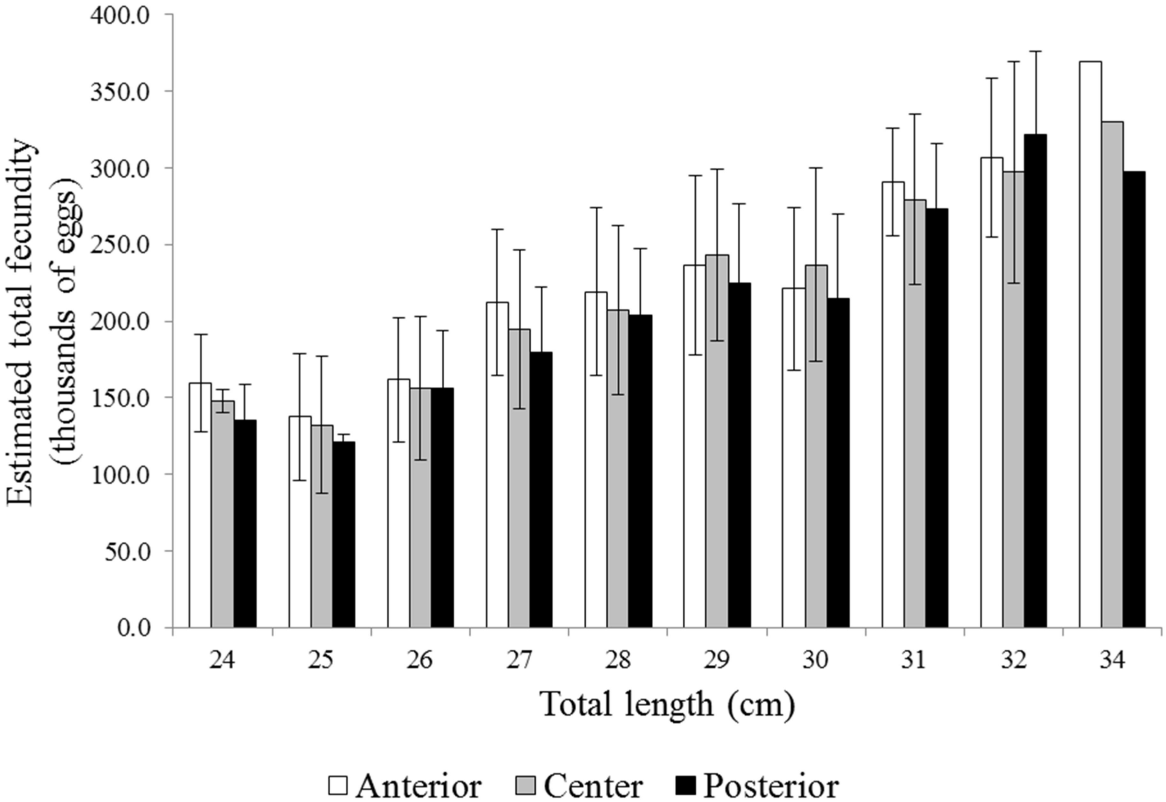

FIGURE 3.6.— Total fecundity estimates at three longitudinal ovary sections (anterior, center, posterior) for each 1-cm bin of total length of Alewives collected in the Lamprey River, Newmarket, New Hampshire. Error bars represent a single standard deviation.

There were no differences between total fecundity estimates of both techniques (Table 3.2). The simple linear regression of $\log_{10}$ total fecundity– $\log_{10}$TL had a good fit (R^2= 0.57) and indicated that fecundity increased with increasing length ($\log_{10}$ F = 2.994($\log_{10}$ TL) - 2.045; N = 69; $P < 0.001$; Figure 3.7A; Table 3.3). The weight-specific fecundity had a better fit to the data (R^2= 0.66) and indicated that total fecundity increased with increasing SW ($\log_{10}$ F = 1.067($\log_{10}$ SW) + 2.778; N = 69; $P < 0.001$; Figure 3.7B; Table 3.3). The strongest relationship of the three models examined was total fecundity-age ($\log_{10}$ F = 1.033($\log_{10}$ Age) + 4.597; $R^{2\,=}$ 0.67; N = 69; $P < 0.001$; Figure 3.7c; Table 3.3). The residual plots of all regressions were randomly

TABLE 3.2.—Total fecundity estimates of Alewife produced using image analysis and Gilson's solution, with ANOVA results of comparison between the techniques. NS indicates no significant difference. NP indicates that due to sample size it was not possible to conduct ANOVA.

	Image analysis			Gilson's solution			ANOVA		
TL bin	N	Estimated total fecundity (thousands of eggs)	SE	N	Estimated total fecundity (thousands of eggs)	SE	F	P	Sig/NS
24-cm	6	147.4	8.6	6	162.5	8.3	0.410	0.588	NS
25-cm	6	130.2	11.6	6	121.0	10.7	0.084	0.800	NS
26-cm	21	157.9	8.7	21	168.4	8.3	0.237	0.635	NS
27-cm	27	195.5	9.2	30	179.7	5.1	0.724	0.407	NS
28-cm	24	209.9	10.1	27	192.8	7.3	0.564	0.465	NS
29-cm	30	235.0	9.9	30	214.7	8.5	0.806	0.381	NS
30-cm	30	224.2	10.2	30	221.4	13.1	0.009	0.924	NS
31-cm	30	280.9	8.1	30	256.0	6.8	2.026	0.172	NS
32-cm	30	308.3	10.8	30	279.5	5.2	2.559	0.127	NS
34-cm	3	332.5	20.8	3	364.9	2.2	NP	NP	NP

TABLE 3.3.—Summary of relationships used to estimate total fecundity, fork length, ovary weight, and egg weight from image analysis for Alewives collected in Lamprey River, Newmarket, New Hampshire. F = fecundity, TL = total length, SW = somatic weight, FL = fork length, OW = ovary weight, EW = egg weight.

Relation	Model	Range of Variable	*N*	SE	R^2
Fecundity (thousands of eggs) versus total length (mm)	$\log_{10} F = 2.994(\log_{10} TL) - 2.045$	240–343	69	2.673	0.57
Fecundity (thousands of eggs) versus somatic weight (g)	$\log_{10} F = 1.067(\log_{10} SW) + 2.778$	135.7–367.0	69	6.787	0.66
Fecundity (thousands of eggs) versus Age (years)	$\log_{10} F = 1.033(\log_{10} Age) + 4.597$	3–8	69	0.148	0.67
Fork length (mm) versus total length (mm)	$FL = 0.867(TL) + 9.3742$	215–307	69	2.356	0.97
Ovary weight (g) versus total length (mm)[a]	$OW = 0.2837(TL) - 52.651$	13.7–48.6	20	1.844	0.68
Egg weight (mg) versus total length (mm)[a]	$EW = 0.0004(TL) + 0.018$	0.08–0.16	20	0.005	0.17

[a] Relationships were used for comparisons to previous studies shown in Table 3.4 where only fish with gonadosomatic indices equal to or exceeding 10 were included.

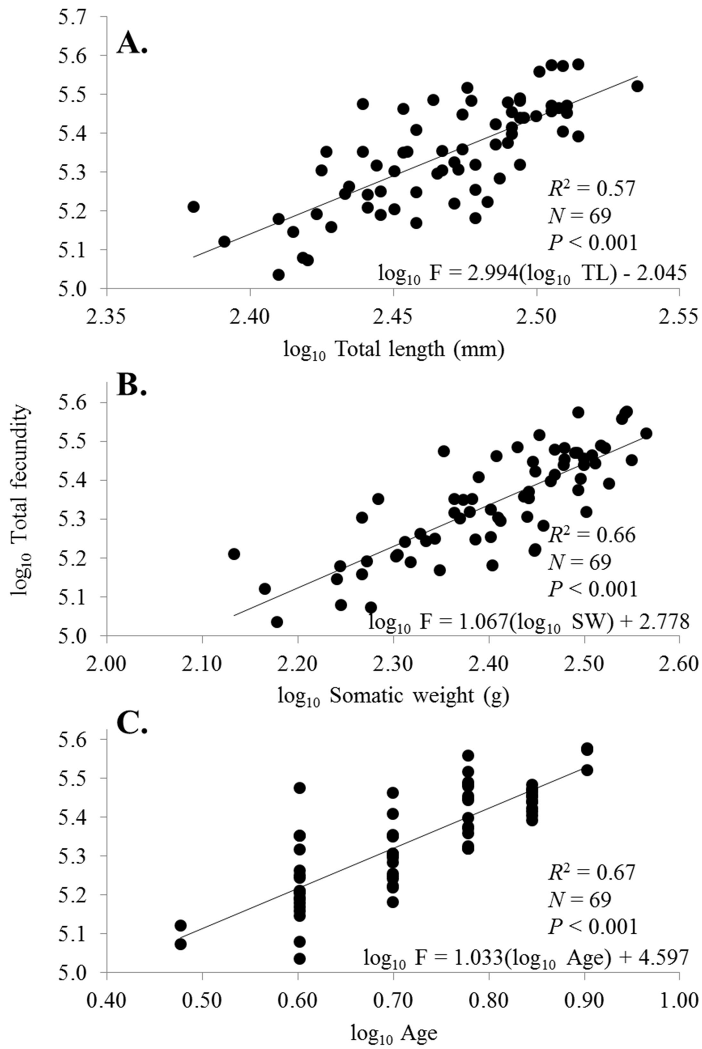

FIGURE 3.7.— Relationships between total fecundity and (A) total length, (B) somatic weight, and (C) age for Alewives collected in the Lamprey River, Newmarket, New Hampshire.

distributed and showed no indications of bias. The quadratic form of the regressions was also fit to the data for the same comparisons, but all showed no increase or a decrease in fit, therefore the simple linear regressions were used.

Discussion

Fecundity studies have traditionally been very time consuming and required viewing and measuring oocyte samples microscopically. In this study, the methodology used to capture oocyte images with a flatbed scanner and analyze with image analysis software, was very effective in identifying, counting and measuring large numbers (662 – 2,699 oocytes/subsample) of oocytes for fecundity estimates without using hazardous Gilson's solution. Oocyte clustering occurred on occasions when formalin was not added to the vials immediately (less than five minutes) after sampling, and required manual separation prior to scanning, even after fixing in solution for six weeks. Samples immediately placed into solution after being weighed, however, provided excellent images for computer analysis. The agreement between fecundity estimates produced on individual fish using both techniques suggests that image analysis should be considered a reliable technique for use in estimating fecundity.

The fish sampled in this study were collected from the first dam on the Lamprey River, located at the head of tide, where they first enter the freshwater section of the river. The comparison of GSI from fish used for estimation of fecundity, as well as additional ovary weights throughout the entire spawning season in 2012, indicated that the ovary weight was stable during the sampling period (Figure 3.4). Crawford et al. (1986) noted that prior to river entry, river herring cease feeding and that oocyte development was essentially complete. Similar to the findings in the current study, Jessop (1993) found no differences in GSI of Alewives sampled from different sections of the spawning river. This suggests that although fish may have begun spawning upriver during the sampling period, all fish sampled at the dam still had total potential fecundity for the season. From oocytes measurements taken from the anterior, center, and posterior section of the ovaries it can be concluded that that there is a relatively homogenous distribution of sizes along the entire length of the ovary. These findings are in agreement with Ganias et al. (2015), who through histological examination of samples from each section, found no difference in oocyte size along the longitudinal axis of the ovary.

A previous study showed that due to the Alewives short spawning season (usually one to two months), the oocytes that will be spawned in that season are fully developed by the time the fish enters freshwater (Crawford et al. 1986). Recent findings however, have concluded that Alewives spawn multiple batches of oocytes in a season, and that oocytes were organized in 4–5 distinct batches of sequential development (Ganias et al. 2015). In a study examining fecundity of New Brunswick and Nova Scotia Alewives (Jessop 1993), it was found that oocytes with diameters smaller than 400 µm would not be spawned during the current season and those remaining from the larger diameters would be reabsorbed by atresia or carried over to the next spawning season. Retention of smaller oocytes indicated that total fecundity values reported by Jessop (1993) are much larger than the number of ripe oocytes that would be spawned, with fertility only being 38% to 67% of total fecundity.

Oocyte diameters from fish sampled in all (1-cm bin) size categories in this study exhibited bimodal diameter peaks of diameters with the first peak of greatest quantity at the threshold of 400 µm. A second peak located at 750 µm was also consistent across all sampled fish, but it appears that over much of the range of lengths (26–32 cm) the two peaks become more similar in percentage of oocytes. Upon approaching the upper extent of their size range a much greater percentage of oocytes are larger than 750 µm (Figure 3.5). Bimodality of Alewife oocyte diameters similar to those in the present study were found previously (Mayo 1974; Huber 1978; Ganias et al. 2015), but Jessop (1993) showed peaks at smaller diameter located at the 200–300 µm and 500-600 µm diameters. The smaller peaks relative to the present study and that of Ganias et al. (2015) are a likely result of extended preservation time in Gilson's solution, which is known to cause pronounced shrinkage in oocytes (Klibansky and Juanes 2007; Ganias et al. 2015).

Results of previous studies river herring studies have shown that in relation to an increase in latitude along the Atlantic coast: (1) total fecundity declines, (2) ovary weight increases, and (3) oocyte weight increases (Kissil 1969, Street 1969; Scherer 1972; Mayo 1974; Loesch and Lund 1977; Jessop 1993). The Lamprey River in New Hampshire falls between the Parker River in Massachusetts and the Tusket River in Nova Scotia. When the total fecundity estimates from the present study using the same estimation methods as Jessop (1993) are added to the existing published estimates, they support to the idea of changes with latitude (Table 3.4).

Previous studies (Mayo 1974; Jessop 1993) of Alewife fecundity found similar results of increasing oocyte weight with fish length and concluding that larger Alewives produce larger oocytes, but this is not consistent in all previous work (Kissil 1969) or in Blueback Herring (Loesch 1969). Results from this study indicate that fecundity increases substantially as the fish age. This finding of age as the best predictor of fecundity in Alewives is contrary to the findings of Jessop (1993), who found age as a nonsignificant predictor. Jessop notes that age is often less useful as a predictor of fecundity due to the high variability in annual growth. Although the fit of the model for age-fecundity was best, it was only slightly better than somatic weight, and all three variables (TL, SW, age) exhibited highly significant relationships ($P < 0.001$). Length and weight measurements can be gathered from fish species quicker and more easily than age. For this reason, the minimal gain in model fit from age data is most likely outweighed by the ease and speed of length and weight collection, in turn making the use of age less likely in many studies.

TABLE 3.4.—Latitudinal variation along the Atlantic coast of North America of fecundity, ovary weight, and egg weight (adjusted to a fork length of 265 mm) of Alewives. (Adapted from Jessop 1993.)

River, state or province	Reference	North latitude	Fecundity	Ovary weight (g)	Egg weight (mg)
Bride, Connecticut	Kissil 1969	41°20'	273,900	33.5	0.13
Parker, Massachusetts	Mayo 1974	42°50'	215,400	30.2	0.13
Lamprey, New Hampshire	Present study	43°05'	211,500	31.3	0.14
Tusket, Nova Scotia	Jessop 1993	43°50'	140,700	33.7	0.24
Saint John, New Brunswick		45°15'			
Mactaquac (1973–1976)	Jessop 1993		142,300	36.9	0.26
Mactaquac (1983–1984)	Jessop 1993		174,900	37.4	0.21
Gaspereau, Nova Scotia	Jessop 1993	45°05'	160,300	30.4	0.19
Margaree, Nova Scotia	Jessop 1993	46°25'	144,700	41.8	0.29

In this study, we took three oocyte samples from each ovary to ensure that there were not developmental differences in oocyte quantity and diameter throughout the ovary. The agreement in oocyte diameter distribution and fecundity estimates across ovary sections, indicate that future research could increase efficiency of sample collection by only sampling a single ovary section from more individuals, rather than three subsamples per individual. Better model fits may also be achieved by reducing the size of the bin from 1-cm to 5 mm as a bin size of 1 cm can include multiple ages, but at smaller growth increments there may be little increase in fecundity.

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APPENDIX A

TABLE A.1.—Detailed movements of all fish radio tagged and released at river left (RL).

Tag #	Time to first detect (min)	Location of first detect	Time spent at antenna location (minutes) A2	A3	A4	A5	A6	From Wadleigh Falls to Wiswall Dam Time (hrs)	Mean speed (rkm/hr)	From Wiswall Dam to Macallen Dam Time (hrs)	Mean speed (km/hr)	Residence time (days)	Pattern of movement
12	15	A2	282		6	84		19.07	0.67				2-4-5
13	15	A2	2,850		3	817	52	37.00	0.35	73.00	0.08	8.29	2-4-5-6
14	17	A2	1,425		5	342	77	32.00	0.40	48.00	0.12	5.21	2-4-5-6
15	15	A2	4,570		4	353	153	27.00	0.47	30.00	0.19	6.46	2-4-5-6
16	16	A2	377	15	5	1,790		6.32	2.03				2-4-3-5
17	15	A2	10,408		5	115	147	59.00	0.22	35.00	0.16	15.00	2-4-5-6
55	15	A2	380		4	850	35	52.00	0.25	74.00	0.08	7.33	2-4-5-6
56	16	A2	1,704		15	1,470		139.00	0.09				2-4-5
57	15	A2	2,772		3	713		34.00	0.37				2-4-5
58	15	A2	1,527	2,078	9	1,026	119	8.92	1.44	27.00	0.21	6.25	2-4-3-4-5-6
59	15	A2	13,411		7	2,330	7	56.00	0.23	13.50	0.41	15.33	2-4-5-6
61	15	A2	4,557		5	1,977	122	40.00	0.32	37.00	0.15	13.04	2-4-5-6
62	15	A2	1,655		4	339	579	8.92	1.44	20.98	0.27	4.54	2-4-2-5-6
63	17	A2	4,702		3	7,828		78.00	0.16				2-4-5
64	16	A2	630	4	4	752	159	29.00	0.44	11.77	0.48	4.17	2-4-3-2-5-6
65	16	A2	11,088		4	125	39	32.00	0.40	4.68	1.20	11.21	2-4-5-6
66	18	A2	####	6,989	123	146	40	18.35	0.70	17.03	0.33	20.17	2-4-3-4-3-4-3-4-3-4-3-4-5-6
67	23	A2	1,583		3	881	11	26.00	0.49	22.72	0.25	4.17	2-4-5-6
68	15	A2	9,478		4	198		35.00	0.37				2-4-5
69	18	A2	3,398		1	0		31.00	0.41				2-4-5
70	15	A2	1,298		5	316		57.00	0.22				2-4-5
71	15	A2	1,478	2,417	185	1,164		27.00	0.47				2-3-4-3-4-3-4-5

TABLE A.2.—Detailed movements of all fish radio tagged and released at river right (RR).

Tag #	Time to first detect (min)	Location of first detect	Time spent at antenna location (minutes) A2	A3	A4	A5	A6	From Wadleigh Falls to Wiswall Dam Time (hrs)	Mean speed (rkm/hr)	From Wiswall Dam to Macallen Dam Time (hrs)	Mean speed (km/hr)	Residence time (days)	Pattern of movement
19	21	A3		3,529	71	1,166	39	6.27	2.04	30.00	0.19	12.33	3-4-3-4-3-4-3-5-6
20	17	A3		7,144	4	143	39	32.00	0.40	6.68	0.84	11.29	3-4-5-6
21	15	A3		6,298	5	1,017	156	17.77	0.72	16.83	0.33	11.21	3-4-5-3-4-5-6
22	16	A3		2,321	7	804	126	5.07	2.53	17.13	0.33	13.29	3-4-3-5-6
23	29	A3		7,668	6	513	23	12.05	1.06	7.28	0.77	12.29	3-4-5-6
24	15	A3		2,333	12	408	20	2.03	6.30	4.35	1.29	12.29	3-4-3-4-3-4-3-4-5-6
25	15	A3		2,623	6	186	175	49.00	0.26	38.23	0.15	11.21	3-4-5-6
26	15	A3		1,821	14	249	67	7.18	1.78	63.25	0.09	7.29	3-4-3-5-6
27	15	A3		3,164	24	0	156					7.46	3-4-6
28	51	A3		3,325	3	405	386	76.00	0.17	30.00	0.18	10.67	3-4-5-6
29	15	A3		1,606	31	587	67	78.00	0.16	42.00	0.13	15.08	3-4-3-4-3-4-5-6
30	15	A3		6,940	7	342		9.02	1.42				3-4-5
72	15	A3		12,580	4	91	41	17.40	0.74	25.00	0.23	14.00	3-4-5-6
73	21	A3		7,144	33	1,082	67	43.00	0.30	20.32	0.28	14.00	3-4-5-6
74	19	A3		550	5	648	76	27.00	0.48	13.83	0.40	4.17	3-4-3-5-6
75	422	A3		4,542	11	1,396	263	3.48	3.67	20.27	0.28	10.92	3-4-3-4-3-4-3-5-6
76	70	A3		6,503	26	208	230	31.00	0.42	18.88	0.30	10.04	3-4-3-4-3-4-5-6
77	15	A3		483	28	1,314	25	27.00	0.47	56.00	0.10	7.38	3-4-3-4-5-6
78	15	A3		1,397	118	638	162	99.00	0.13	31.00	0.18	10.04	3-4-3-4-3-4-5-6
79	746	A3		11,618	3	351	58	28.00	0.46	22.15	0.25	14.08	3-4-5-6
80	15	A3		220	9	1,459	85	75.47	3.69	46.00	0.12	5.17	3-4-3-5-6
81	15	A3		714	9	1,338	38	29.00	0.45	60.00	0.09	7.13	3-4-5-6
82	15	A3		11,013	2	395	17	29.00	0.44	31.00	0.18	16.17	3-4-5-6
83	15	A3		1,767	9	1,853	73	66.00	0.19	6.47	0.87	13.04	3-4-3-4-3-4-5-6

TABLE A.3.—Detailed movements of all fish radio tagged and released at Brady Farm (BF).

			Time spent at antenna location (minutes)					From Wadleigh Falls to Wiswall Dam		From Wiswall Dam to Macallen Dam			
Tag #	Time to first detect (min)	Location of first detect	A2	A3	A4	A5	A6	Time (hrs)	Mean speed (rkm/hr)	Time (hrs)	Mean speed (km/hr)	Residence time (days)	Pattern of movement
32	165	A4		2,936	5	491	56	93.00	0.14	15.95	0.35	11.42	4-3-4-5-6
33	212	A4		2,356	53	2,301	11	71.00	0.18	43.77	0.13	15.25	4-3-4-3-4-3-5-6
34	164	A4		8,606	15	894	49	2.08	6.14	45.12	0.12	13.17	4-3-4-5-6
35	466	A4	3,360		38	25		8.53	1.50				4-2-4-5
36	1,376	A3		0		226	189	13.93	0.92	22.67	0.25	4.38	3-5-6
37	927	A3		0		488	158	7.70	1.66	22.60	0.25	4.33	3-5-6
39	2,763	A3		0		313	0	37.00	0.35				3-5
40	1,994	A3	0	0		1,092	182	33.00	0.38	5.52	1.02	12.25	3-2-3-5-6
41	395	A3	2,715	20,136	70	292	118	9.03	1.42	2.87	1.95	23.13	3-4-3-4-2-4-5-6
42	2,116	A5				689	87	35.00	0.36	46.98	0.12	4.33	5-6
43	2,512	A5				781	21	42.00	0.31	18.32	0.31	4.96	5-6
44	174	A4		7,892	12	560	98	9.12	1.40	4.68	1.20	10.42	4-3-4-5-6
45	187	A4		2,154	4	0		0.00					4-3-4
47	395	A3		0	0	2,305		5.32	2.41				3-5
48	1,320	A3	0	0		1,196		51.00	0.25				3-2-5
49	196	A4		3,447	23	17		6.88	1.86				4-3-4-5
50	232	A4			0	1,570	128	32.00	0.40	32.25	0.17	9.21	4-5-6
51	1,020	A5				1,504	110	17.00	0.75	25.65	0.22	3.71	5-6
52	676	A3		0	0	835		25.00	0.51				3-5
53	190	A4		8,569	14	46		7.33	1.75				4-3-4-5

TABLE A.3.—(continued).

Tag #	Time to first detect (min)	Location of first detect	Time spent at antenna location (minutes) A2	A3	A4	A5	A6	From Wadleigh Falls to Wiswall Dam Time (hrs)	Mean speed (rkm/hr)	From Wiswall Dam to Macallen Dam Time (hrs)	Mean speed (km/hr)	Residence time (days)	Pattern of movement
54	4,949	A5				4,782	569	82.00	0.16	18.00	0.31	10.71	5-6
84	260	A4		4,304	197	111	104	51.00	0.25	22.82	0.25	9.21	4-3-4-3-4-5-6
86	1,062	A5				1,424	40	17.70	0.72	63.08	0.09	6.33	5-6
87	330	A3		0		813	96	71.00	0.18	8.40	0.67	7.33	3-5-6
88	3,674	A5				784	46	61.00	0.21	47.38	0.12	5.42	5-6
89	295	A3		0		422	15,997	5.52	2.32	20.13	0.28	31.00	3-5-6
90	1,005	A5				563	82	16.75	0.76	20.58	0.27	3.33	5-6
91	1,696	A5				670	14	28.00	0.45	22.63	0.25	3.29	5-6
93	1,643	A3		0		326	352	12.68	1.01	20.97	0.27	3.75	3-5-6
94	397	A3		0		106	128	33.00	0.38	23.05	0.24	3.29	3-5-6
95	8,617	A5		249		184	56	144.00	0.09	30.22	0.19	7.42	3-5-6
96	165	A4		9,709	18	141	174	13.63	0.94	20.32	0.28	10.50	4-3-4-5-6
97	188	A4		8,354	11	122	161	30.00	0.42	4.88	1.15	11.46	4-3-4-5-6
98	2,360	A5				852		39.00	0.33				5
100	253	A4		21,569	99	377	57	17.87	0.72	3.63	1.54	23.13	4-3-4-3-4-5-6
101	94	A2	0	60	25	547	77	33.00	0.39	20.87	0.27	3.33	2-4-3-4-5-6
103	2,478	A4		5,256	8	549	57	12.10	1.06	21.67	0.26	13.25	4-3-4-5-6
104	1,896	A5				1,496	37	32.00	0.41	25.08	0.22	4.38	5-6
105	2,058	A3		0		389	44	67.00	0.19	25.17	0.22	8.33	3-5-6
106	1,176	A3		0		334	143	17.20	0.74	51.23	0.11	4.54	3-5-6

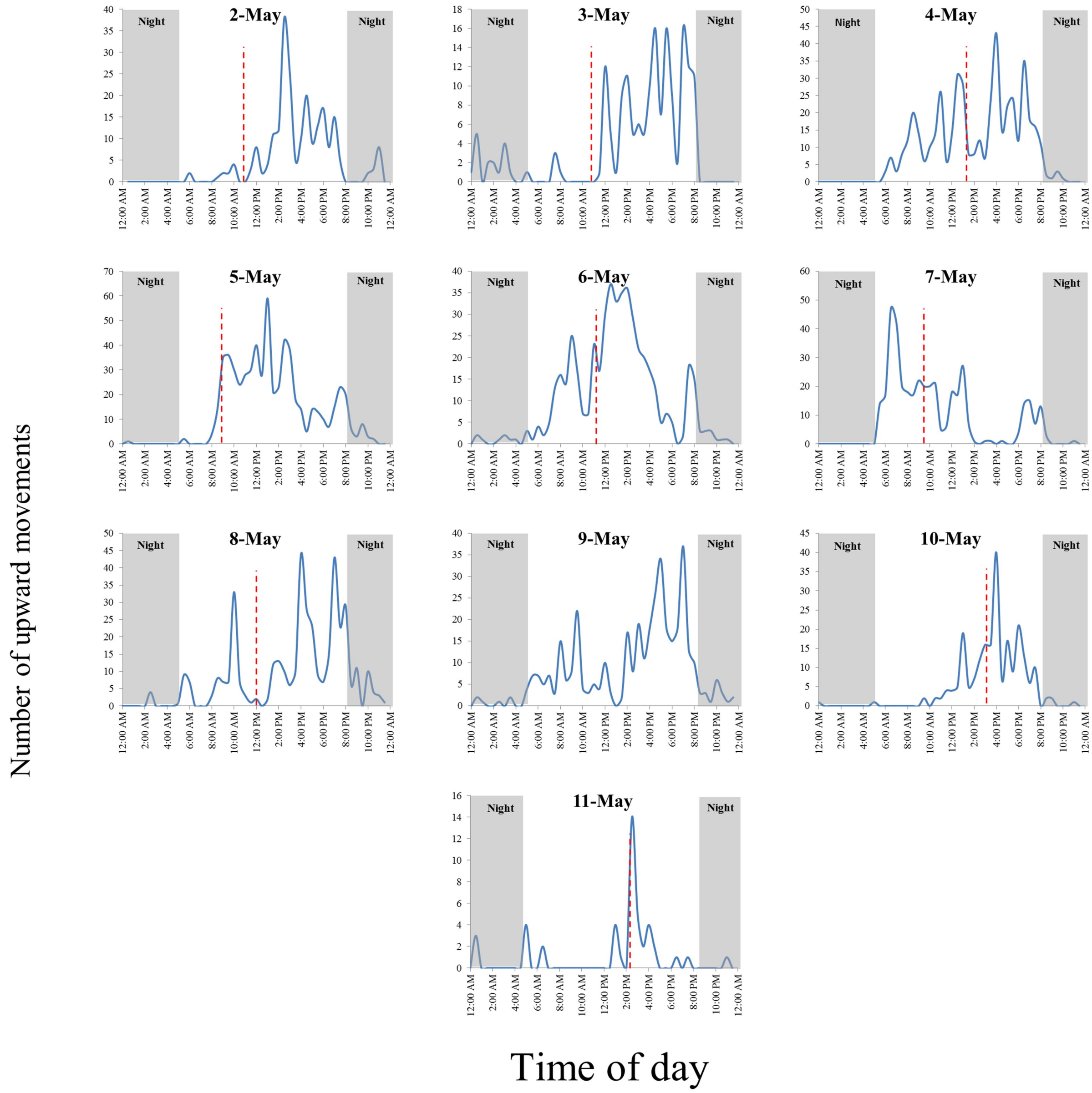

FIGURE A.1.—Number of upward movements of tagged fish to the nearest half hour between May 2 and May 11, 2013. Areas shaded in gray are nighttime hours and dashed lines indicate the time the trap at the top of the fishway was physically emptied by net.

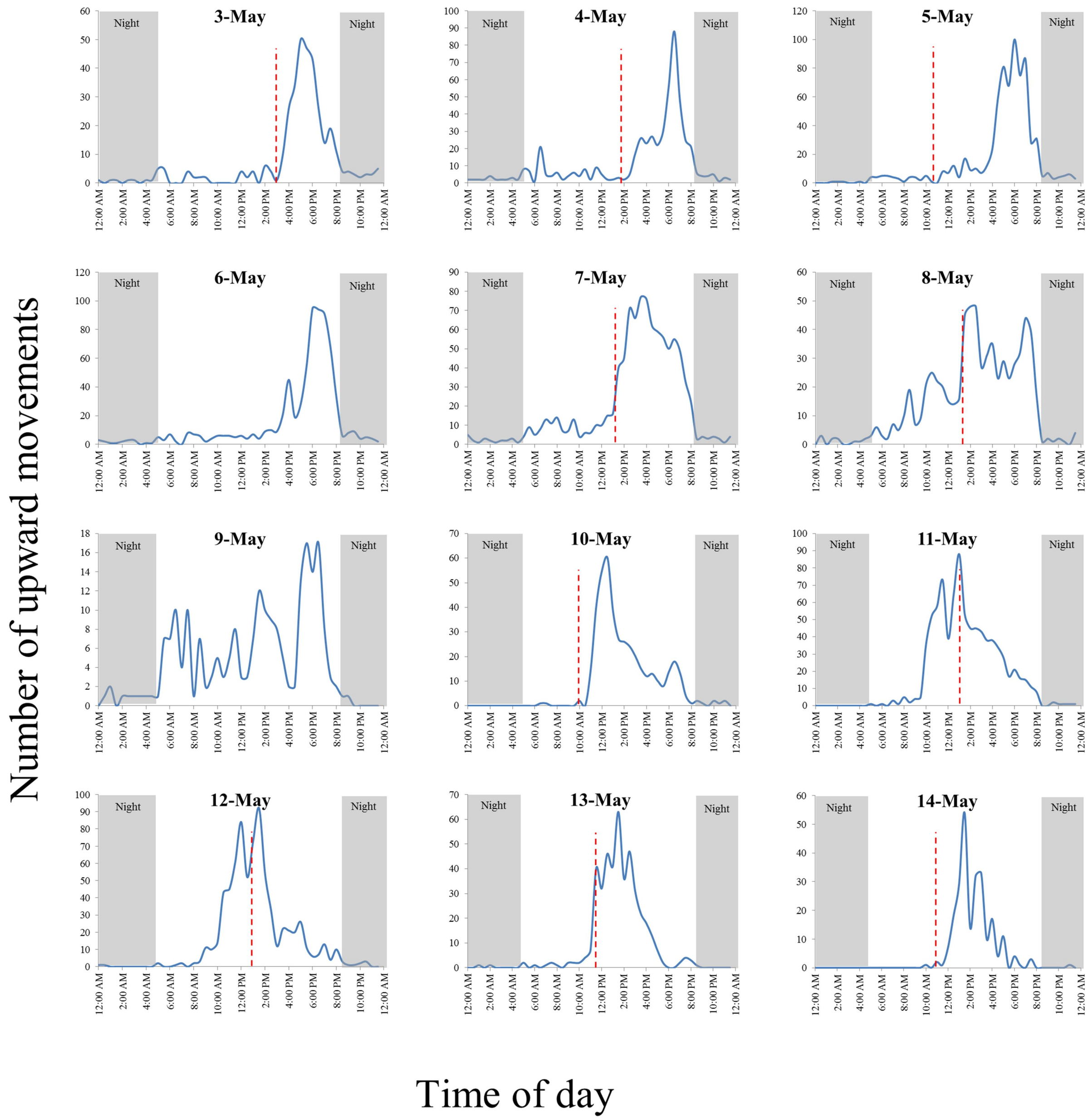

FIGURE A.2.—Number of upward movements of tagged fish to the nearest half hour between May 3 and May 14, 2014. Areas shaded in gray are nighttime hours and dashed lines indicate the time the trap at the top of the fishway was physically emptied by net.

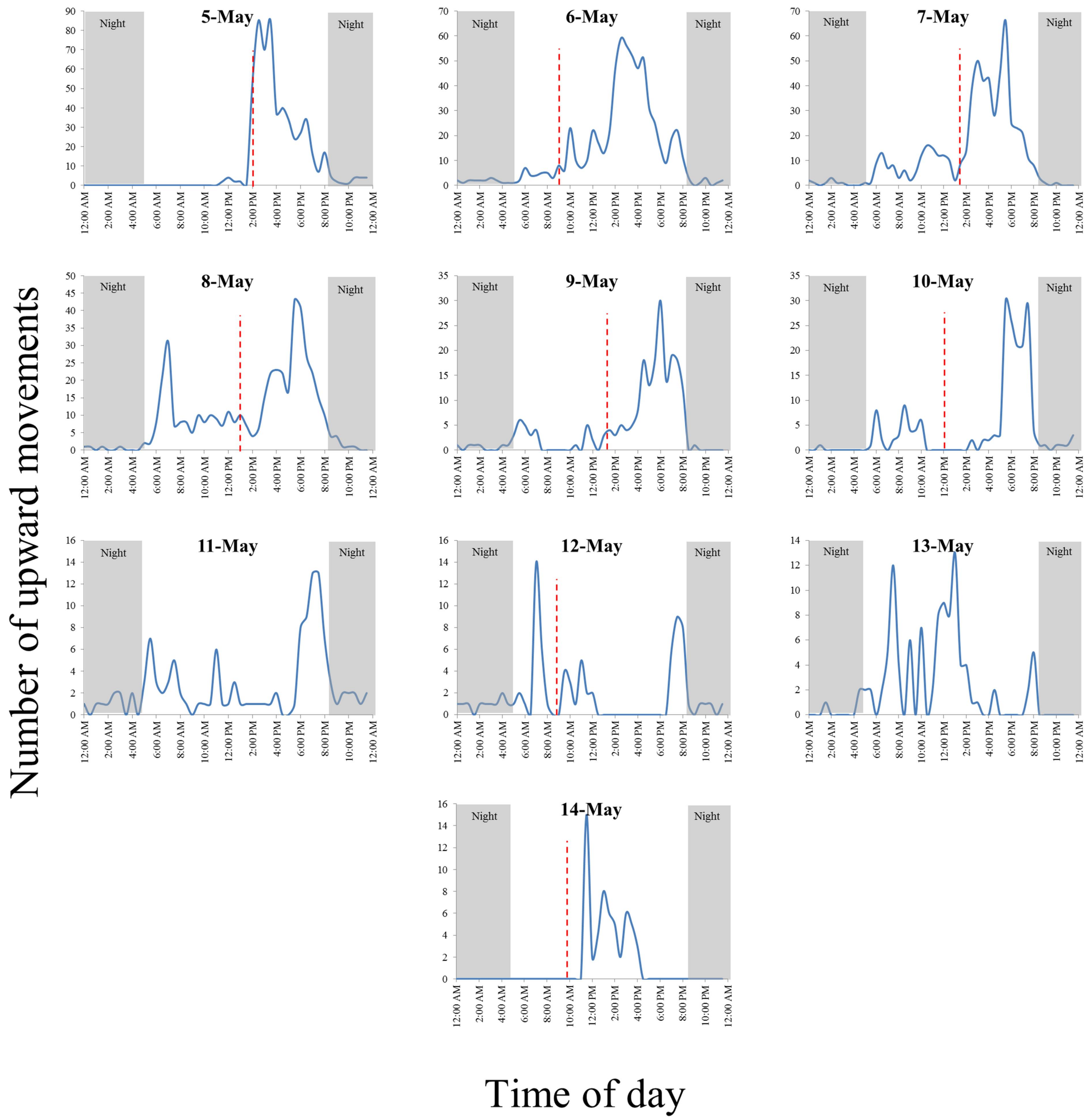

FIGURE A.3.—Number of upward movements of tagged fish to the nearest half hour between May 5 and May 14, 2015. Areas shaded in gray are nighttime hours and dashed lines indicate the time the trap at the top of the fishway was physically emptied by net.

APPENDIX B

University *of* New Hampshire

Research Integrity Services, Service Building
51 College Road, Durham, NH 03824-3585
Fax: 603-862-3564

21-Mar-2013

Berlinsky, David L
Biological Sciences, Rudman Hall
Durham, NH 03824

IACUC #: 120404
Project: River Herring Aquaculture and Population Assessment
Category: D
Next Review Date: 25-Apr-2014

The Institutional Animal Care and Use Committee (IACUC) has reviewed and approved your request for a time extension for this protocol. Approval is granted until the "Next Review Date" indicated above. You will be asked to submit a report with regard to the involvement of animals in this study before that date. If your study is still active, you may apply for extension of IACUC approval through this office.

The appropriate use and care of animals in your study is an ongoing process for which you hold primary responsibility. Changes in your protocol must be submitted to the IACUC for review and approval prior to their implementation.

Please Note:
1. All cage, pen, or other animal identification records must include your IACUC # listed above.
2. Use of animals in research and instruction is approved contingent upon participation in the UNH Occupational Health Program for persons handling animals. Participation is mandatory for all principal investigators and their affiliated personnel, employees of the University and students alike. Information about the program, including forms, is available at http://unh.edu/research/occupational-health-program-animal-handlers.

If you have any questions, please contact either Dean Elder at 862-4629 or Julie Simpson at 862-2003.

For the IACUC,

Jill McGaughy

Jill A. McGaughy, Ph.D.
Chair

cc: File